EVOLUTION

ESSAYS ON ASPECTS OF EVOLUTIONARY BIOLOGY

PRESENTED TO

PROFESSOR E. S. GOODRICH

ON HIS

SEVENTIETH BIRTHDAY

EDITED BY

G. R. DE BEER

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PREFACE

THE services which Professor Goodrich has rendered to Zoology during nearly half a century of outstanding and uniformly productive work are common knowledge. As regards his written contributions to biological science, this will be clearly apparent from the list of his scientific works which is appended.

It will be noticed that there is scarcely a group of the animal kingdom to which Professor Goodrich has not turned his attention, and there is no group which, his attention turned to it, has not thereby benefited by a lasting contribution of knowledge. Nor have the subjects and problems of embryology, genetics, homology, evolution, and other theoretical aspects of the subject been neglected by him. As Editor of the *Quarterly Journal of Microscopical Science* since 1921 he has performed a service of inestimable value to almost all branches of Biology.

After considering the ways in which the appreciation by zoologists of Professor Goodrich's work might most suitably be given expression, I decided to attempt the production of a Congratulatory Volume to be presented to him on the occasion of his seventieth birthday. The decision to prepare a planned volume on a definite subject under a single title, instead of a collection of separate and unco-ordinated investigations, was deliberate since such a volume would in itself be more valuable as a contribution to science. In the search for a suitable subject, I owe to Dr. Julian Huxley the suggestion of the title actually adopted, *Evolution*, as being a field in which Professor Goodrich has always been deeply interested and to which so many of his works have made notable contributions.

It is necessary for me to explain the manner in which this book has come into being, because its nature has necessitated a strict plan and the selection of a limited number of authors to cover as evenly as possible the various more important aspects of modern knowledge concerning evolution. I have been successful in securing the collaboration of twenty such authors, from among Professor Goodrich's past or present colleagues or pupils. While selecting them I have been conscious

of the fact that many eminent Oxford zoologists were being omitted, but the plan and scope of the book to be written allowed me no other course. At the same time, there are many persons who have been glad to associate themselves with our congratulations to Professor Goodrich, as the List of Subscribers to this volume shows.

The royalties derived from the sale of this work will be placed at the disposal of the Board of the Faculty of Biological Sciences which, through the Biological Scholarship Committee, will devote them to grants to students from Professor Goodrich's Department wishing to study at the laboratories of the Marine Biological Association, or the Freshwater Biological Association, or other approved institutions.

We therefore offer this work to Professor Goodrich as a token of our gratitude and esteem, and with our most sincere wishes that he may long continue to direct his Department, and increase still further the indebtedness to him of all zoologists.

G. R. DE B.

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21 *June* 1938.

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INSECT ADAPTATION AS EVIDENCE OF EVOLUTION BY NATURAL SELECTION

By SIR EDWARD POULTON

THE choice of a suitable subject for this paper was a rather difficult problem, but I finally decided to bring together certain observations on insect life which appeared to demand a Darwinian and exclude a Lamarckian interpretation, closing with the proof that the same conclusions, based on the same kind of evidence, had been fully reached by Henry Walter Bates only two years after the publication of the *Origin of Species*. My own observations and the educational experience which led to them recall memories of the department which Professor Goodrich has so successfully and happily administered during seventeen years, and in which he has laboured since 1891 when he joined his friend and former teacher Ray Lankester. It will only be possible to refer very briefly to a few of these early memories, but I feel that they ought not to be altogether omitted.

The most absorbing interest of my life, from boyhood, has been derived from the observation of insects in their natural surroundings and in the study of their life-histories and reactions to changing conditions, by means of breeding experiments. For one who in youth had few opportunities of visiting other countries, this study was a fortunate choice, inasmuch as the light which it sheds upon the motive causes of evolution is strong and clear. It was probably in some respects also an advantage that, in Reading, my native town, as it was before the beginning of movements which led to the University, a young naturalist, restricted to the companionship of a few kindred spirits, was for the most part thrown back upon himself and the compelling interest of his subject. A great change came in 1873 when I travelled to Oxford three days a week and worked for a scholarship in Professor George Rolleston's department in the University Museum, a department which, in those early days, included not only Zoology and Comparative Anatomy, but

also Human Anatomy and the germs of the present departments of Anthropology, Animal Physiology, and Biochemistry (then called Physiological Chemistry and later Chemical Physiology). Suddenly entering these bewilderingly interesting and exciting surroundings, presided over by the most outstanding personality I had ever encountered, many happy years of work as a student and young graduate here passed without, however, any serious attempt to undertake original research. I cannot resist the temptation to recall one memory of 1876 when I caught an adder at Folkestone and packed it off to Charles Robertson[1] who taught us Histology and would, I felt sure, be glad to examine the poison glands. I heard afterwards that the label, 'Live adder inside', caused some consternation, but the unfortunate reptile, which did not survive the journey, contained young from which Mr. Robertson hoped to prepare sections.

During these years I devoted as much time as could be spared to the insects in the Hope Department where Professor J. O. Westwood was always most kind and helpful, and I continued to collect and breed insects, especially in the Long Vacations. After taking my degree in December 1876 I became Junior Demonstrator under Rolleston and thus began to know intimately and to learn much from my old friend W. Hatchett Jackson, the Senior Demonstrator, who called my attention to A. R. Wallace's *Essays on Natural Selection*, published in 1870. My copy of the second edition (1875) is inscribed 1878—the year when I read and was deeply stirred by two of the papers: 'III. Mimicry, and other protective resemblances among animals', and 'IV. The Malayan Papilionidae or Swallow-tailed Butterflies, as illustrative of the theory of Natural Selection.'

Rolleston died in 1881 and was succeeded by his old pupil H. N. Moseley who in the Summer Term of 1882, when he first came into residence, most kindly suggested that I should work on material which he had collected on the 'Challenger'. Thus for some years all the time I could spare from teaching and my beloved insects was devoted to the tongues of Marsupials and *Ornithorhynchus*, leading on to the bill, hair, ovary, and teeth of the latter archaic form. I can never forget the

[1] The series of beautiful dissections on which Rolleston wrote *Forms of Animal Life* were prepared by Charles Robertson.

generosity with which Dr. Kitchin Parker treated a young man half his age, who had found these teeth in sections borrowed for the pursuit of another investigation.[1] These mammalian papers, published for the most part in the *Quarterly Journal of Microscopical Science*, led to the beginning of a lifelong friendship with Ray Lankester, who took Moseley's place during his long illness and succeeded him as Professor.

Thoughts upon the evolution of insect adaptations, aroused by Wallace's Essays, were carried further when August Weismann's *Studies in the Theory of Descent* was translated by Raphael Meldola and published in 1882. Charles Darwin, who wrote a brief preface to the volume, concluded with the words:

'Finally, whoever compares the discussions in this volume with those published twenty years ago on any branch of Natural History, will see how wide and rich a field for study has been opened up through the principle of Evolution; and such fields, without the light shed on them by this principle, would for long or for ever have remained barren.'

Weismann's researches, described in the second part of this volume, *The Origin of the Markings of Caterpillars* (pp. 161–389), together with Meldola's valuable notes, supplied the stimulus which led to the beginning of work upon the evolution of insect adaptations. I was especially attracted because the author had selected as the subject of his investigations the larvae of Hawkmoths (Sphingidae). I had always been deeply interested in these beautiful caterpillars and had reared several of them from the egg, so that Weismann's careful description of the changes undergone by the markings during larval life, their biological value and evolution by natural selection, together with the objections to an interpretation founded upon a supposed internal developmental force ('phyletic vital force') at once appealed to me, leading to a re-study of an old subject in a new light, and to a series of papers on the colours, markings, and attitudes of insects. The first of these,[2] read in 1883 before the Entomological Society of London, led to the beginning of a close, life-long friendship with the Secretary, Professor Raphael Meldola. Professor Moseley also very kindly sent to me the encouraging letter he had received from Weismann, who was

[1] *Viriamu Jones and other Oxford Memories*, Poulton, London, 1911, pp. 236–41.
[2] Published in *Trans. ent. Soc. Lond.*; pt. i, April 1884, pp. 27–60, Pl. I.

interested in the results of work suggested by his own researches. Throughout the whole of these investigations I was convinced that the protective adaptations had been evolved by natural selection and in 1898 brought together many lines of evidence to prove that Mimetic and Warning Colours had arisen in this way.[1]

Towards the end of this last paper brief mention was made of the controversy on the supposed hereditary transmission of acquired characters which arose when the eight essays, written 1881–8, by Professor Weismann, became well known.[2] Our friendship with the author, initiated by the kindness of Professor Moseley, had grown with the work on insects and a deepening interest in heredity; he was staying with us in 1887 before the meeting of the British Association, and we travelled to Manchester together and spoke in the discussion on the question, 'Are Acquired Characters Hereditary?', introduced by Ray Lankester—a discussion in which Hubrecht, Patrick Geddes, and Marcus Hartog also took part. Although the communications then made are not printed in the Report of the Meeting, the English translation of Weismann's Essays appeared in 1889 and his conclusions became widely known—conclusions, said by Professor Goodrich in his Address to the Zoological Section of the British Association at Edinburgh in 1921, to be 'the most important contribution to the science of evolution since the publication of Darwin's *Origin of Species*'. At the Bath meeting of the Association in 1888 a long discussion with a dear friend, the late Professor H. F. Osborn, led me to realize that Lamarckian evolution, based on the transmission of acquired characters, was the prevalent belief firmly held in his country, and I longed for the opportunity of visiting America and of taking part in a debate on the subject. In the meantime it appeared desirable to publish a general account of recent work on insects

[1] *J. Linn. Soc. Lond.—Zool.*, **26**, 558. Reprinted, with many additions, in *Essays on Evolution*, Poulton, Oxford, 1908, p. 220.

[2] Abstracts of the first two essays (1881 and 1883) by Sir Peter Chalmers Mitchell were published in *Nature*, **37**, 541–2 (1888), and **38**, 156–7 (1888); an account of the third (1883), by A. E. Shipley in *The Nineteenth Century*, for May 1885; of the fourth and fifth (1885 and 1886) by H. N. Moseley in *Nature*, **33**, 154–7 (1885), and **34**, 629–32 (1886); the sixth (1887) by Weismann himself in *Nature*, **36**, 607–9 (1887). The seventh and eighth both appeared in 1888, the year before the English translation of the complete series, by A. E. Shipley, Selmar Schönland, and the present writer, was published in 1889.

and its bearing upon evolution, in the hope of stimulating fresh researches. In this book[1] the special suitability of insects for an inquiry into the motive cause of evolution is briefly explained on pp. 264, 265:

'The defenceless character of the group as a whole, the extent to which they are preyed upon by the higher animals, their enormous fertility, and the rapidity with which the generations succeed each other, are reasons why natural selection operates more quickly and more perfectly than in other animals, producing mimetic resemblances or other forms of Protective Resemblance in number and fidelity of detail unequalled throughout organic nature.'

A few years later the longed-for opportunity came and I was able to visit America and take part in a discussion, held 7 February 1894, by the Boston Society of Natural History. I propose to recall only a single argument against a Lamarckian interpretation of evolution, but it is one which, so far as I am aware, has never been refuted or indeed noticed by Lamarckian writers. Adaptive instincts displayed by the prey of animals much larger than themselves cannot have arisen by gradual improvement based upon hereditary experience. A caterpillar in spinning its cocoon has no chance of learning by experience. The test of success or failure will come much later—generally in winter when insect-eating animals are pressed for food. In such instances, and they are very numerous, we are compelled to believe that survival has been made possible by prophetic instincts which provide, not for experience of enemies but for complete avoidance by enemies—instincts which can only have developed on Darwinian lines.[2]

At the Leeds Meeting of the British Association in 1890 I showed in an evening lecture examples of the adaptations which had been described and classified in *Colours of Animals*, and I venture to recall a friendly conversation which took place on the following day between my old friend the late Professor Patrick Geddes, the late Lord Rayleigh, and myself. Geddes argued that the resemblances between mimicking butterflies and their models were accidental. 'They were just thrown off

[1] *The Colours of Animals, their Meaning and Use especially considered in the Case of Insects.* Lond., 1890. Internat. Sci. Series.

[2] Other arguments brought forward in the discussion may be found in *Essays on Evolution*, pp. 110–19.

the wheel', as he expressed it—'phases which had to be passed through in the lives of species' and happened to be alike. I replied that the models frequently belonged to groups, such as the Danainae, which 'threw off the wheel' various types of widely differing patterns which were followed by distantly related butterflies as well as by moths. Lord Rayleigh, however, gave a much simpler and more trenchant answer—'How would you apply your explanation', he said, 'to the resemblance of insects to bark, or twigs, or leaves?'[1]

It is very interesting to observe that Lord Rayleigh had here, and probably independently, been following the reasoning of Henry Walter Bates, who on p. 508 of his classical paper on Mimicry[2] wrote:

'I believe . . . that the specific mimetic analogies exhibited in connexion with the *Heliconidæ* are adaptations—phenomena of precisely the same nature as those in which insects and other beings are assimilated in superficial appearance to the vegetable or inorganic substance on which, or amongst which, they live. The likeness of a Beetle or a Lizard to the bark of the tree on which it crawls cannot be explained as an identical result produced by a common cause acting on the tree and the animal.'

My copy of this great memoir belonged to Alfred Russel Wallace, who generously gave it to me. It bears the inscription: 'Mr. A. R. Wallace from his old travelling companion the author', and the last sentence of the passage quoted above has been emphasized by pencil side-lines. The paper was read before the Linnean Society on 21 November 1861, two years after the appearance of the *Origin of Species*, on 24 November 1859. A footnote on p. 495 states that 'the materials on which this memoir is founded were collected by the author during eleven years' research on the banks of the Amazons'.

I do not think that Bates has received all the credit owing to one who had so fully and so quickly absorbed the teachings of the *Origin*, a result probably caused in part by the rather severe title which reveals nothing of the far-reaching significance of his introductory pages. The statement on p. 502 that the

[1] A fuller account of this conversation is given in *Proc. ent. Soc. Lond.*, 1925 (1926), pp. xciv, xcv.

[2] *Contribution to an Insect Fauna of the Amazon Valley.* LEPIDOPTERA: HELICONIDÆ'. *Trans. Linn. Soc. Lond.*, **23** (1862), pt. iii (1862), Mem. xxxii, pp. 495–566, Pls. 55, 56.

resemblances to the *Heliconidæ* is the most interesting part of their natural history, and the table of models and mimics (both butterflies and moths) on p. 503 are of course well known; also the following passage on p. 507, to which Wallace had added a blue side-line:

'These imitative resemblances, of which hundreds of instances could be cited, are full of interest, and fill us with the greater astonishment the closer we investigate them; for some shew a minute and palpably intentional likeness which is perfectly staggering. I have found that those features of the portrait are most attended to by nature which produce the most effective deception when the insects are seen in nature. The faithfulness of the resemblance, in many cases, is not so striking when they are seen in the cabinet. Although I had daily practice in insect-collecting for many years, and was always on my guard, I was constantly being deceived by them when in the woods.'

The concluding pages of this paper are devoted to passages quoted from Bates's memoir, passages which show how fully the principle of natural selection was accepted by him as the motive cause of evolution; also others which prove that he rejected alternative attempts to provide an interpretation.

Pp. 507–8. 'It is not difficult to divine the meaning or final cause of these analogies. When we see a species of Moth which frequents flowers in the daytime wearing the appearance of a Wasp, we feel compelled to infer that the imitation is intended to protect the otherwise defenceless insect by deceiving insectivorous animals, which persecute the Moth, but avoid the Wasp.' [Emphasized by Wallace.] The paragraph continues: 'May not the Heliconide dress serve the same purpose to the *Leptalis*? Is it not probable, seeing the excessive abundance of the one species and the fewness of individuals of the other, that the Heliconide is free from persecution to which the *Leptalis* is subjected?'

Bates then maintained in the next paragraph that these mutual resemblances 'cannot be entirely due to similarity of habits or the coincident adaptation of the two analogues to similar physical conditions', although he had found 'the general colours of many widely different species affected in a uniform way in the interior of the South American continent. But this does not produce the specific imitation of one species by another;

it only prepares the way for it.' To this last sentence Wallace had not only added side-lines but 'Good!'

The next paragraph, on the same p. 508, begins with the sentence, also emphasized by Wallace: 'It is perhaps true that the causes (to be discussed presently) which produce a close or mimetic analogy cannot operate on forms which have not already a general resemblance, owing to similarity of habits, external conditions, or accidental coincidence'; but, while admitting this, Bates maintained that 'a close specific analogy' between, e.g. a moth and a bee, could not arise this way. 'It would mean an adaptation of the Moth with especial reference to the Bee.' This is followed by the paragraph quoted on p. 6 and by many examples of Protective Resemblance, some already well known, others observed by him on the Amazons. Among them he mentions the resemblance of insects to the excrement of birds and caterpillars, and suggests that they 'should be carefully considered by those who would be inclined to think that the object of mimetic analogies in nature was simply variety, beauty, or ornament: . . .' (p. 509). To these examples he adds many and varied instances of insect mimicry, concluding with his well-known description of a very large caterpillar which resembles a small poisonous snake. This and almost all the other examples have been emphasized by Wallace. The conclusion to which they lead is stated on p. 510: 'I think it will be conceded that all these various kinds of imitative resemblances belong to the same class of phenomena, and are subject to the same explanation. . . . All are adaptations, either of the whole outward dress or of special parts, having in view the welfare of the creatures that possess them.'

He then discussed, on pp. 510, 511, the evidence that some species of the Heliconidae are specially protected and 'enjoy by some means immunity from effective persecution, and that it is therefore an advantage to others not so fortunate, and otherwise unprovided for, if they are so like as to be mistaken for them', continuing in the next paragraph: 'The process by which a mimetic analogy is brought about in nature is a problem which involves that of the origin of all species and all adaptations.' Admitting that he was unable to explain the local variation of the models, Bates continued—'With the mimetic species . . . the case is different. . . . The existence of the species,

in each locality, is seen to depend on its form and colours, or *dress*, being assimilated to those of the *Ithomiæ* of the same district, which *Ithomiæ* are changed from place to place, such assimilation being apparently its only means of escaping extermination by insectivorous animals. Thus we have here the reason why local races are formed out of the natural variations of a species: the question then remains, how is this brought about?'

'The explanation of this seems to be quite clear on the theory of natural selection, as recently expounded by Mr. Darwin in the 'Origin of Species'.' Then, after discussing (on pp. 511, 512) the direct action of physical conditions and sudden evolution 'in one generation by *sports* or a single act of variation', he continues, 'It is clear, therefore, that some other active principle must be here at work to draw out, as it were, steadily in certain directions the suitable variations which arise, generation after generation, until forms have resulted which . . . are considerably different from their parent as well as their sister forms. This principle can be no other than natural selection, the selecting agents being insectivorous animals, which gradually destroy those sports or varieties that are not sufficiently like the *Ithomiæ* to deceive them.'

After further discussion, which would occupy too much space, he concluded as follows on p. 513: 'Such I conceive, is the only way in which the origin of a mimetic species can be explained. I believe the case offers a most beautiful proof of the truth of the theory of natural selection. It also shows that a new adaptation, or the formation of a new species, is not effected by great and sudden change, but by numerous small steps of natural variation and selection.'

On the subject of chance likenesses Bates wrote in a footnote on p. 514: 'Some orders of insects contain an almost infinite variety of forms, and it will not be wonderful, therefore, if species here and there be found to resemble each other, although inhabiting opposite parts of the earth, and belonging to widely different families. Such analogies are accidental, and can have nothing at all to do with the evidently intentional system of resemblances, carried on from place to place, which I have discussed.'

In the following final paragraph (pp. 514, 515) of the intro-

ductory section the author again expresses his conviction that natural selection offers the true interpretation of evolutionary histories for which innate tendencies or Lamarckian desires had been invoked, while his deeply significant opening lines offer a convincing interpretation of appearances which have seemed to suggest these hypotheses:

'The operation of selecting agents, gradually and steadily bringing about the deceptive resemblance of a species to some other definite object, produces the impression of there being some innate principle in species which causes an advance of organization in a special direction. It seems as though the proper variation always arose in the species, and the mimicry were a predestined goal. This suggested the only other explanations that I have heard of, namely, that there may be an innate tendency in the organization to become modified in a given direction—or that the parent insect, being powerfully affected by the desire of concealment from the enemies of its race, may transmit peculiarities to its offspring that help it to become modified, and thus, in the course of many generations, the species becomes gradually assimilated to other forms or objects. On examination, however, these explanations are found to be untenable, and the appearances which suggest them illusory. Those who earnestly desire a rational explanation, must, I think, arrive at the conclusion that these apparently miraculous, but always beautiful and wonderful, mimetic resemblances, and therefore probably every other kind of adaptation in beings, are brought about by agencies similar to those we have here discussed.'

THE PRESENT STANDING OF THE THEORY OF SEXUAL SELECTION

By J. S. HUXLEY

Introductory

NONE of Darwin's theories have been so heavily attacked as that of sexual selection. As a matter of fact, the theory as enunciated in 1871 was a remarkable achievement, considering the state of biological ignorance at the time. In the first place, he had to rely very largely, in some groups almost entirely, on the bare circumstantial evidence of structure, and secondarily, the general theory of animal coloration was still in its infancy. Accordingly, as a result of the undeveloped state of the subject, he persistently attached too much weight to the view that bright colours and other conspicuous characters must have a sexual function.

This ascription was further encouraged by the ignorance then prevailing as to the facts of the hereditary process. By a wholesale application of the supposed 'law' of the transference to one sex of characters evolved by the other, he was able to include in his rubric of display-characters all those in which both sexes are equally or almost equally conspicuous.[1] So strongly did he believe in this that after adumbrating a process of mutual sexual selection, he rejected it in favour of unilateral sexual selection followed by transference.

Also unknown in 1871 were many facts concerning the restriction of display in many species to the period after mating-up has occurred, e.g. in birds the importance of territory, the initiative often taken by the female in soliciting coition, &c., which again necessitate modifications in the theory.

Finally, Darwin had not thought out the full implications of the distinction between intra- and inter-specific selection.

[1] Transference, total or partial, to one sex, of characters originally developed in the other, does of course occur (see, e.g., Meisenheimer [35, chap. 23]; Winterbotham [57]); but we are still very much in the dark as to the genetic-evolutionary mechanisms involved, so that it is dangerous to hypothecate any 'force' or 'tendency' making for transference.

Nevertheless, it is well to remember the extent of Darwin's positive achievement. He gave the biological reason for the existence of weapons and greater strength and size in the males of many species, in the shape of what may be called the struggle for reproduction; and for the bright colours and special structures used in display, in the shape of their action as stimuli to the behaviour of the opposite sex. He further showed that combat- and display-characters confined to one sex could be developed in ways useless or even deleterious to the species; and that the operation of selective principles would lead to the male sex generally diverging more from the ancestral stock than the female, and often being more variable. And the enormous body of facts which he collected has served as a basis for all subsequent investigators.

Thus there are really two quite distinct bases for Darwin's theory as developed in *The Descent of Man*, the first deductive, the second inductive:—1. A struggle between males for success relative to other males in reproduction (intra-sexual selection). 2. The possession of certain types of character by one sex (or even both sexes). These are almost exclusively characters supposed to subserve either combat or display, and their possession is regarded as a proof that sexual selection of the intra-specific type defined by Darwin has been at work.

In what follows I shall review various ingredients of Darwin's theory, in the light of modern knowledge.

The function of Conspicuous Characters

It is in regard to display that the main controversy has raged.

1. Criteria for asserting that characters (structures and/or actions) have been specially evolved to subserve the function of display before the other sex. (*a*) They must be striking. (*b*) They must be actually employed in display, i.e. in the presence of members of the opposite sex, and in such a way as to be conspicuously perceived by them. (*c*) They must be sufficiently complex to make it certain that they are not merely by-products of physiological excitement but must have been specially evolved.

Darwin was often content with (*a*) and (*c*). This, however, is quite insufficient. Many characters satisfying these requirements have since been shown to subserve quite other functions, such as threat, deflexion, recognition, warning, &c.

With regard to (*a*) it is clear that none but a striking display could be expected to be effective. On the other hand, display actions may be quite striking without the presence of brilliant colours or special structures, e.g. in many of the warblers. (*b*) Careful observation will always make it clear whether this condition is fulfilled. When so, it is possible to say that the display is directed *at* the member of the opposite sex. Further, when bright colours or special structures (plumes, wattles, &c.) occur, they are rendered specially prominent by the display-action. When this is not so, as with the bright body-colours of male ducks, it is illegitimate to postulate their evolution in relation to display.

This does not exclude the possibility of display occurring in the absence of all members of the opposite sex; sexual excitement may overflow thus even in solitary males, or may be diverted to abnormal objects.

Nor does it exclude the possibility that the actions should also subserve other functions in other circumstances, e.g. threat as well as display in the oyster-catcher (Huxley and Montague [23]), though this is rare. Conspicuous structures, however, are often used to subserve different functions, notably display and threat, but in different ways.

2. Criteria for distinguishing characters evolved in relation to epigamic display from those subserving other functions involving conspicuousness.

All such characters are *allaesthetic*, i.e. characters which become effective via the sense-organs and brain of other organisms (see Huxley [21]). These fall into two broad groups—those promoting inconspicuousness (cryptic), and those promoting conspicuousness (sematic). All epigamic characters fall into the latter class;[1] so do those concerned with threat, warning, false warning (Batesian mimicry), recognition, and deflexion. Inter-individual (social) deflexion, as exemplified by the 'injury-feigning' of many birds (Jourdain, [24]; Saunders, [49]), or by the bright colours of many male ducks, of the male Bulwer's pheasant (Heinroth [12]) or the delayed moult of certain male ptarmigan, rendering them, we may say, abnormally conspicuous and so deflecting the attention of

[1] With the one exception, so far as I am aware, of the pre-mating actions of male mantids (see later).

predators from the females during the period when they are biologically more valuable, can be included.

Biologically functional conspicuousness can then be cross-classified as follows, always remembering that the alternatives may intergrade: (i) (*a*) into characters permanently or at most times conspicuous and not rendered prominent merely in relation to a special situation. Among these we can place the bright colours of many male birds, such as finches, ducks, orioles, chats, &c., which are not specially revealed during display; most true songs; the distinctive markings of the males in species with sexes otherwise alike (e.g. flickers, &c.: Noble [39], Noble and Vogt [41]); the distinctive patterns of birds which spend most of their time on the wing; warning colours like those of wasps, coral snakes,[1] &c. These are all adapted to act at a distance (though this does not exclude their employment at close range).

(i) (*b*). Characters not at most times conspicuous but displayed conspicuously in relation to particular types of situation; among these are most obvious epigamic display characters, e.g. in birds of paradise, peacock, *Machetes*, or egrets; warning characters such as the use of the rattle by rattlesnakes, or the filaments and false eyes of the puss-moth caterpillar; recognition characters that are only revealed when in alarm or in flight; threat characters such as those of the male Gelada baboon, or of male lizards (Noble and Bradley [40]), &c. Such characters are, in general, adapted to be effective at short range, in relation to past or future action by an enemy, a rival, a mate, or a member of the group.

A second method of classification is as follows: (ii) (*a*) those adapted primarily to arrest attention; (ii) (*b*) those adapted primarily to stimulate emotion. Among the former will be found characters subserving recognition, deflexion, distance warning, and distance threat. Among the latter are those threat and warning characters adapted to elicit fear; e.g. bristling of manes, 'terrifying' action of puss-moth, dominance threat of baboons (Zuckerman [58]), &c.; and also characters adapted to arouse sexual emotion, i.e. true epigamic displays.

Clearly all characters designed to arrest attention must be

[1] For examples, see Poulton [44].

as immediately conspicuous as possible; thus, when visual, they must be simple patterns of strongly contrasting shades or colours (Lorenz [32]). The type of pattern will further differ according as to whether it is adapted to conspicuousness at a distance or at short range; short-range characters can clearly afford to be more detailed, to cover a smaller area, and to be less strikingly patterned.

There is a further important difference between characters whose conspicuousness is adaptively distinctive to a single group and those whose conspicuousness is adaptively shared by many species.

With the latter category biologists have long been familiar in the shape of warning and false warning (mimetic) colours. The interest of the former type of character, however, is only now beginning to be realized. Here the *principle of distinctiveness* (Lorenz [32]) is at work. It will operate wherever it is an advantage to restrict the response to the character to members of a single group, usually to those of the same sex, species, or related group of species. This will occur with most types of recognition marks, notably with those which enable young individuals to recognize adults of their own species (Molony [36]), and those serving for sex recognition and for challenge and threat between rivals.

The probability is very great that in higher animals such characters serve as barriers to mating between related species whose areas overlap. The most striking cases are those where visual appearance is almost identical but song strikingly different, for instance the willow warbler and the chiffchaff. Undoubtedly the same process has been at work when colour-pattern is strikingly dissimilar in related species of similar size and proportions, &c., blackbird and thrush, stonechat and whinchat.

However, even when there can be no question of fertile cross-mating, distinctiveness will be an advantage whenever prompt response to an advertisement is advantageous, and when the response is useless if given to members of another species concerned with reproductive functions—sex recognition, rivalry, and threat.

Clearly, there will be a marked difference in type between shared and distinctive patterns in the two cases. With shared

conspicuousness the pattern may be extremely simple, e.g. alternating segments of yellow and black for warning. In the latter case, the pattern must still be conspicuous and therefore bold, but must have a sufficient number of components to permit of their *arrangement* being distinctive and easily recognizable.

Many writers have commented on the extraordinary diversity shown by the markings of related brightly coloured species, whether restricted to one sex or found equally in both sexes. This is the inevitable outcome of Lorenz's principle of distinctiveness, which will encourage difference for difference's sake.

Finally, we come to those characters adapted to eliciting emotion. Those concerned with promoting fear will either make their possessor more formidable, by increasing its apparent size, or will be preparatory to or symbolic of actual fighting; or will mimic a dangerous enemy; or finally will enhance general terrifying appearance by means of bizarre markings or structures (white eyelids of male Gelada baboon, probably many facial patterns of birds, &c.: see Hingston [13]).

Those concerned with sexual stimulation may again be actions preparatory to or symbolic of coition (the antics of numerous male birds in display); or they may display special structures of a striking nature (train of peacock, &c.).

In general, and especially in the sexual group, distant conspicuousness is not so important as with characters concerned with arresting attention. Characters, however striking and however specific, which we can be sure are employed solely or mainly in display to the other sex, are usually beautiful and delicate rather than distinctively conspicuous at a distance (e.g. peacock, Argus pheasant, peacock pheasant, plumes of birds of paradise and egrets). Even such brilliant creatures as the male Amherst pheasant show an elaboration of detail which is lacking in patterns obviously of the distinctive-conspicuous type, e.g. oriole, reed bunting. In such cases, however, the two functions may well be combined, the broad outlines of the pattern being distinctively conspicuous at a distance, the details effective in display.

In numerous other cases, the same structure may be employed, but in different ways, for threat and for display (ruff of *Machetes* or of great crested grebe; male plumage in black-

cock, &c.); the resultant type of character will then naturally tend to be a compromise.

So far as I am aware, this point, of the distinctions to be expected between the type of patterns subserving distance threat (and sexual recognition), short-range threat, and epigamic display respectively, has not previously been made. Distance threat and recognition will promote highly distinctive conspicuousness; short-range threat of a non-symbolic nature will promote bizarre conspicuousness, not so broadly patterned or so distinctive; epigamic display will promote striking patterns and structures not necessarily distinctively conspicuous at a distance, and, in general, more remarkable for delicacy, pleasing detail, and what we must call beauty.

Darwin's ascription of an aesthetic sense to female birds and other organisms has been bitterly attacked. However, both he and his critics have referred to the supposed action of such an aesthetic sense the origin of many characters which have quite other functions than display. With our present knowledge it seems that Darwin's view was in principle correct.

Physiological effects of display

Darwin was inclined to limit the possible effects of display to the psychological sphere (e.g. female choice of mates), but the discovery of the intimate dependence of reproductive functions on emotional states and other higher cerebral functions now points to the possibility of important physiological effects, such as earlier maturation of the gonads, more effective ovulation, synchronization of male and female rhythms, &c. It is true that this applies mainly to birds, but birds (very possibly for this reason) provide most of the good examples of epigamic display. F. H. A. Marshall in his Croonian Lecture [33] and Fraser Darling in a recent book [4b] have covered different aspects of this problem.

Harper [10], followed by Whitman [55] and Martin [34], has shown the extreme importance of this psycho-physiological effect. He found that virgin pigeons and doves, while normally not ovulating if kept alone, would do so if they were kept in the same cage with another female, in an adjacent cage to a male, or sometimes when caressed on the head by the

human finger. Marshall [33] has summarized the data on the subject, pointing out that the effect must pass through various exteroceptive sources via the brain to the anterior pituitary.[1] Many birds will only attempt to breed in captivity when the correct nest-material is provided; others (ground-nesters) only when the correct background (e.g. gravel of a certain type) is available. Lack [28] has found that with Arctic terns the nest-site may be decisive. If the ground is flooded or water-logged from late snow-melting, ovulation may be inhibited for over three weeks, doubtless through visual stimuli acting on the pituitary.

A. A. Allen [1] has carried out experiments which show that in ruffed grouse both males and females have a limited period ('oestrus') during which successful fertilization is possible, that when captive-reared males in the correct phase (as determined by their readiness to attempt coition with stuffed specimens) are placed with females, a considerably higher fertility-rate is obtained (94 per cent. of eggs fertile as against about 70 per cent., the fertility-rate in the wild being about 90 per cent.), than if males and females are put together at random. One of the two displays performed by the species is not epigamic but to do with threat or dominance over rivals, and defeat in combat has far-reaching general effects, birds though physically uninjured sometimes dying as a result, if not promptly removed from contact with other birds, and even when physically recovered losing the impulse to mate for the rest of the season. Conversely, successful threat-displays promote both general and sexual vigour, and epigamic displays stimulate the female's reproductive physiology.

An interesting case is recorded by Steinbacher [52]. Three male pelicans (*P. onocrotalus*) in the Berlin Zoo, kept in one enclosure with a single female, showed much display activity in May and June 1937. They developed the visible epigamic characteristics of the species—frontal protuberance and orange-yellow colour of the bare skin near the eye. The female paired with one of the males. The frontal protuberance of the successful male became larger, while those of his two unsuccessful

[1] He further points out that in mammals ovulation (in species where this is normally dependent on coition) and pseudo-pregnancy (in other species) can be effected by electrical stimulation of the brain or cord, doubtless via the pituitary.

rivals regressed, their bare eye-skin at the same time becoming much paler in colour.[1]

It is a well-known fact that if several sticklebacks are kept in an aquarium, the male that is successful in combat retains his brilliant nuptial colouring, while those that are beaten lose most of their brilliance.

Recently Darling [4b] has made the important discovery that in breeding colonies of gulls of different size, but of the same species and in the same restricted locality, increased numbers promote slightly earlier onset of laying, and definitely briefer total period of laying in the colony. Apparently there is a cumulative excitement serving to stimulate and therefore to synchronize the oestrus period and the onset of ovulation. The phenomenon was observed both in the herring gull and the lesser blackbacked gull, in spite of the fact that the colonies of the latter were comparatively scattered. Apparently to compensate for this fact, however, the birds of this species gathered for social display in a small area of the breeding-ground.

Mr. D. Seth-Smith tells me that it is well known to aviculturalists that budgerigars breed much better when a number are kept together than when isolated by pairs.

Howard's [16, 17] painstaking observations indicate that there exist short-period physiological rhythms connected with readiness to mate, as well as the more basic physiological cycle, which latter is mainly important in the female, leading to ovulation; and he suggests that display actions are largely directed to the synchronization of these minor rhythms. Marshall [33] draws attention to the harmful effects of the cessation of selection for synchronization in some domestic animals: e.g. in the horse the oestrus period is much longer than that during which fertilization is possible, and fertility is only about 50 per cent.

It is probable that both Howard's views and those of Allen and of Darling are correct, and that display is capable of stimulating or regulating all aspects of reproductive physiology and behaviour.

[1] The yellowish feathers round the pouch showed the same phenomena; Steinbacher suggests that they owe their colour to contamination with the secretion of the preen-gland, which would apparently not be so much employed by the unsuccessful males.

Huxley [20], referring to Howard's observations that the females of many passerine birds show two levels of sexual behaviour (the former inducing an interest in the males and permitting of pairing-up and of early stages of nest-building but not of coition, the second supervening a few days before the first egg is laid, and associated with readiness to copulate and with building the lining of the nest), suggests that these may be correlated with the two physiological phases discovered by Riddle in the growth of the avian oocyte, the second phase being a short one of great intensity, initiated by a marked change in endocrine balance.[1] He further suggests that male display in monogamous birds, by promoting the endocrine change needed to realize the final growth of ova, may have a selective effect in counteracting the depressing psycho-physiological effect of cold and wet weather on ovulation, which is reflected in the observed fact of a lower average size of clutch in bad seasons. Effective display would then promote a higher number of ovulations than would otherwise occur. Beebe [2] has insisted that display must have a psycho-physiological effect on reproductive processes, though the precise mechanism suggested by him is certainly incorrect. These suggestions are borne out by Darling [4b], who finds in gulls that the psycho-physiological effect of numbers on reproductive processes is relatively greater in bad seasons.

So-called 'self-exhausting' displays (Huxley [18]; Southern [51]) which do not normally lead to coition, may really be stimulative in regard to reproductive function, as well as serving as an emotional bond attaching the members of a pair.

Natural versus sexual selection in relation to display

The facts recorded in the previous section indicate that display may often be of advantage to the species in promoting more effective reproduction. Any resultant selection will therefore come under the head of Natural Selection, not Sexual Selection in Darwin's sense.

In general, it has now become clear that the hypothesis of

[1] Allen [1] similarly records that female ruffed grouse show a definite change in behaviour (initiation of special posturing and of nest-construction) six days before the first egg is laid; and virgin pigeons (Harper [10]) will usually lay about eight days after being subjected to stimulation by a male's display.

female choice and of selection between rival males irrespective of general biological advantage is inapplicable to the great majority of display characters. Darwin himself pointed out that many secondary sexual characters must have originated through natural selection, e.g. organs for catching and holding females prior to and during copulation. The same, of course, applies to copulatory organs, although for some curious reason Darwin hardly refers to these at all. In some cases it is known that female orgasm is needed for ovulation to occur (rabbit), and this may probably be deduced in others from the existence of special stimulating organs on the penis (see Meisenheimer [35, chap. 12]). Here the parallelism would seem to be complete with the similar function of male display, which may thus with justice be spoken of as a 'psychological penis'. This is borne out by Sturtevant's work [53] on *Drosophila*. He found experimentally that the male's wing-display promoted a much higher degree of successful fertilization, by inducing readiness to mate in females; but that it had no relevance to female choice, since when a normal male and a male with his wings cut off were placed in a tube with a single female, the wing-clipped male was accepted almost as readily as the intact one, but much more frequently than if he had been confined alone with a female.

To all such characters, Poulton's [44] term *epigamic*, originally applied only to display coloration, may be legitimately extended. Epigamic will then denote all characters subserving the union of the gametes. They will include characters of the gametes themselves; of the gonads; of the male and female copulatory organs, ducts, and accessory glands; of male prehensile organs; of organs facilitating the discovery or recognition of one sex by the other; and finally display activities stimulating reproductive behaviour.

A slightly different function of display is concerned rather with the number of young produced than with securing fertilization, and is thus reproductive rather than epigamic. It will be of importance in cases, e.g., where display stimulates ovulation.

Intra-specific selection

By intra-specific selection (see Haldane [9]) we mean selection as between different individuals of the same species, as

opposed to inter-specific, between individuals of different species. Inter-specific selection obviously must promote the biological advantage of the species. Intra-specific selection, on the other hand, though it may also act thus, may in certain circumstances favour the evolution of characters which are useless or even deleterious to the species as a whole. This will happen when groups, all of one species, are isolated from competition with any other species, as occurs prenatally between members of one litter in polytocous placental mammals (Haldane's intra-familial selection). It will happen when large numbers of a species occur together to the total or virtual exclusion of ecological competitors. For instance, with dominant plant species, notably trees, competition will be almost wholly intra-specific, notably in the growing stages, and will promote characters such as rapid growth in early stages. Dominant species among densely living ciliary-feeding animals will be in similar case as regards feeding mechanisms. Even when specific and individual advantage on the whole coincide, intra-specific selection may push adaptation to levels of perfection which must be useless to the species (hypertely), e.g. in some cases of cryptic and mimetic resemblance.

But the most extreme examples concern reproduction. This is what one would expect, since reproductive advantage can have a more rapid evolutionary effect in promoting the spread of a beneficial character than advantage as between individuals of a single generation. An obvious example is the profusion of spermatozoa in animals or of pollen-grains in plants. This is most marked in forms which liberate their gametes wholesale, but the amazing profusion of blossom in entomophilous trees, where transport of the gametes is not dependent upon chance, reminds us how strong the selective intensity must be.

Finally, we come to Darwin's sexual selection, i.e. competition between males for reproductive advantage. Here again inter-male competition may promote specific as well as individual advantage, e.g. with most secondary sexual characters concerned with display and threat in monogamous species. Occasionally, however, characters useless to the species may be promoted even in such forms; e.g. the earlier appearance of males on the breeding areas in monogamous birds, notably those where territory is of biological importance (see Howard

[14, 15]). With simultaneous arrival of the sexes, the available territory would doubtless all be taken up, so that total reproduction would be unaffected; but an early male will be more likely to secure territory than a late arrival. Male arrival is thus pushed back as far as possible, the limit being decided by food supply and climatic factors, so that insectivorous migrants will be only a few days in advance of the females, while resident forms can and do take up their territories much earlier (Howard [15]).

For the females, on the other hand, with the greater dependence of their reproductive functions on external conditions, it will be disadvantageous to leave their winter feeding-grounds too early.

But extreme intensity of inter-male competition will only be found when polygamy can occur. In monogamous forms, the advantage of a male display or other secondary sexual character is limited by the normal breeding capacity of one female. But in polygamous forms (using the term in its widest sense) the limit possible to a successful male is not the maximum reproductive output of one female but of many. Selective intensity may therefore achieve far greater heights than in monogamous forms; and it is no coincidence that in polygamous forms alone do we find display-characters pushed to a limit at which they are clearly useless to the species as such and may sometimes be deleterious to the ordinary struggle for existence. We may compare the ruff of *Machetes*, the train of the peacock, the tail of the Argus pheasant, or the plumage and display actions of birds of paradise, with similar characters in monogamous types, e.g. the ruff of the great crested grebe, the display actions of male Sylviidae, or the aigrette plumes of egrets (references in Huxley [19]).

The same is true of characters concerned with rivalry and combat between males. Combat and its apparently universal concomitant threat occur between males in monogamous just as much as in polygamous species. But since the advantages of success and therefore the selective intensity are higher where polygamy prevails, it is only in such forms that characters subserving combat and threat are developed to an exaggerated degree. Characters of this sort may be of three main types—those affecting mere strength and size, those concerned with

threat, and special weapons concerned with actual combat; though, of course, one character may embrace more than one function. As regards size, males are frequently distinctly bigger than females (though, as Darwin [5] pointed out more than half a century ago, this is uncommon in insects, where males rarely fight for mates, but rely on swift discovery of them); but extreme size-dimorphism related to combat is only seen in polygamous types, e.g. the sea-elephant. Exaggerated threat-characters may be illustrated by the ruff of the polygamous *Machetes*, though this also subserves display; and exaggerated weapons by the antlers of male deer and the tusks of male elephants, although those undoubtedly also subserve distance threat.

For selection of this type, between individual males, it will be best to substitute the term *intra-sexual selection*, noting that it will not reach extreme intensity except in polygamous forms.

Correlation of mode of life and type of organization with type of sexual behaviour

The most obvious correlations of this sort are the greater development of display characters and weapons in polygamous forms, and the evolution of display in relation to the level of sensory and cerebral capacity, both noted by Darwin himself. But there are many others.

Adequate analysis has so far only been attempted with birds. In a preliminary study (Huxley [19]), the following main points were demonstrated: (1) The inverse correlation of conspicuous coloration with need for concealment. (2) The enhancement of display (and threat) characters with polygamy. (3) The correlation of sex-limitation of display and threat characters and actions with reproductive behaviour. These are limited to the male where only the female broods and cares for the young; better developed in the female when the male alone broods and cares for the young; and shared, in large measure or completely, by both sexes when both parents share in brooding and in feeding the young (and then normally continued throughout the season with the additional function of an emotional bond between the pair). (4) In species with mutual display, the occurrence of display at the nest-site in powerful colonial species, away from the nest-site in species

where the eggs need protection from predators. (5) The correlation of type of display or threat with habitat; e.g. aerial flight-songs in territorial birds of open country, flight displays in strong flyers, diving displays in diving birds, &c. (6) The correlation of distance threat and advertisement characters with territoriality (songs and bright colours of male passerines).

We may now add the following: (7) In territorial species, the correlation of threat-characters shared by both sexes with the holding of winter territory by both sexes (red-breast). (8) The correlation of male deflexion characters with monogamy (or family-group polygamy) in which the male remains near the nest (and sometimes also near the young), but is of less biological value than the female as he neither broods nor cares for the young (various ducks and game-birds). (9) The correlation of three distinct types of polygamy with three different methods of origin: (*a*) family-group polygamy (jungle-fowl, some pheasants); this arises among precocial birds where the male does not incubate, but remains near the nest and young, and is correlated with high development of display and threat characters; (*b*) territorial polygamy (corn bunting—Ryves [48], some weaver-birds—Lack [29]); this arises among territorial passerines by a single male defending several territories instead of one, and is correlated with no special character-developments except greater territorial alertness; (*c*) mating-group polygamy (promiscuity), (ruff, blackcock, probably birds of paradise, &c.); this arises among forms with semi-social display, and is a natural extension of the fact (see Fraser Darling [4b]) that some species utilize the reproductive advantages conferred by the cumulative effect of numerous individuals' display and threat. This semi-social display occurs in colonial nesters (herons, herring gulls), semi-colonial nesters with special display area (lesser blackbacked gulls), in solitary nesters which exist in flocks up to the moment of nesting (hawfinch, Nicholson [37]; oyster-catcher, Huxley and Montague [23]) and in forms where females visit the stance of a dominant male for mating purposes (ruffed grouse, &c.). Mating-group polygamy, however, seems only to arise when a special area away from the nest is utilized for social rivalry and display, and not in colonial nesting forms.

The physiological effect of socialized sexual emotion enables

us to assign a biological value to the 'piping parties' of the oyster-catcher, whereas previous work (Huxley and Montague, op. cit.) had to be content with analysis of their mechanism. Dense multi-nesting (as in quaker parrakeets and some weaver-birds) is doubtless itself often in part an outcome of this advantage. Mating-group display leads to the development of characters subserving both threat and display (ruff), or to some subserving threat and others display (birds of paradise). (10) The frequent inverse relation of visual and auditory distinctive characters in related species found in the same area. Where appearance is very similar, or birds are very skulking, song tends to be distinctive (chiffchaff and willow-wren; lesser whitethroat; grasshopper warbler; wren; cirl and yellow buntings; sedge- and reed-warblers). Where song is similar or males take up prominent positions, visual characters tend to be distinctive (black-cap and garden-warbler; stonechat and whinchat).[1] (11) The correlation between the presence or absence of sex-recognition characters (visual or auditory) and type of reproductive behaviour. Where the sexes are very distinct, or where they are alike but differentiated by one distinctive character (flickers, Noble and Vogt [41]), epigamic and threat actions are normally quite separate. Where the sexes are similar, sex-recognition is usually effected by trial and error (Lorenz [32]), a simple primary male action eliciting different responses according to whether the individual approached be male or female, and further action being different according to this response.

The type of epigamic character evolved, however, will also differ according to the level and type of organization of the animal involved. The lowest level which need concern us is that of metazoa without mating, i.e. forms which liberate their gametes into the water without association with a particular individual of the opposite sex. Secondary sexual characters will not arise in such forms. Fertilization is ensured by chance, aided by some degree of synchronization of liberation of gametes. This may reach a high degree of precision, as in the palolo worm and other forms with lunar periodicity.

The first adumbrations of 'courtship' are also seen in some

[1] Frequently, of course, both visual and auditory characters are distinctive (reed-bunting, many finches, blackbird, &c.).

polychaetes, in the social gatherings found at mating time. The actions of the worms at these times appear to be mutually stimulative, resulting in a still finer synchronization in the discharge of gametes.

Unilateral display and intra-sexual rivalry appear when the sexes are associated for the purpose of mating, i.e. when internal fertilization occurs, or when, though gametes are liberated into the water, the discharge of male gametes occurs in relation to the fertilization of the gametes of one particular female. In most forms the association of the sexes is for this purpose only; their association for other functions, involving true family life, constitutes a further stage, e.g. the formation of polygamous family bands as in deer or baboons, or of monogamous families as in most birds.

We will begin with the lower stage, without family life. The male's carrying of the female for long periods, so as to be certain of fertilization when the ova are liberated, is confined to this level. Also confined to this stage is the method seen in social hymenoptera, of a competitive pursuit-flight; here selective pressure in favour of efficient eyes and great powers of speed in the males must be very high.

Also distinctive of this stage is the high development of adaptations for the discovery of one sex by the other at a distance, as the main device for securing mating. The astonishing olfactory capacities of the antennae of certain male moths are the outstanding example, while the glow-worm's light and the powerful sounds emitted by cicadas and grasshoppers illustrate the same thing in the visual and auditory spheres respectively. Such mechanisms may be combined with continued prehension, as in Anura. The searching may be done by either sex, or by both.

The pulmonate gastropods are among the highest hermaphrodite animals. It is interesting to find in some of them a unique mechanism for mutual tactile stimulation, in the shape of the *spiculum amoris*.

Display at this level seems almost always to be unilateral, employed only by the male.[1] Sometimes this is definitely

[1] A few cases of mutual display in insects are recorded by Richards [46], e.g. the fly *Empis trigramma*. Most of the insect examples here cited are taken from Richards's very useful summary.

stimulative, engendering a readiness to mate in the female. That seen in newts is of great interest. It is elaborate, involving both visual and olfactory stimuli. When successful its effect is to induce the female to take up the spermatophore previously deposited by the male. The wing-display of *Drosophila* also comes into this category, as presumably does the liberation of perfume by certain male butterflies and by *Hepialus*. In all these cases there is no question of choice of mates by the female; the display merely induces readiness for coition. Tactile stimulation (tapping the female's hind wings with the head) is employed by the common small tortoiseshell butterfly *Vanessa urticae*, and the stridulation of some small grasshoppers serves as an auditory excitant. Visual stimulative display seems to occur in the dragon-fly *Hemiphlebia mirabilis*. An interesting case of 'vestigial display', probably correlated with reduced reactivity of the females, is seen in the rare functionless males in the agamic generation of certain gall-flies (Patterson [43]).

The elaborate communal display (normally combined with combat and rivalry) seen in certain polygamous (promiscuous) birds also falls logically into this category, though historically it must be regarded as secondarily derived from the final level of organization (see below).

Slightly different from stimulative display (though the two categories grade into each other) is display serving to advertise the existence of a sexual situation. This would seem to exist mainly in forms with a comparatively low level of nervous organization, in the behaviour of which only a few kinds of situations are possible. The classical case is the brandishing by the male fiddler-crab of his enormously hypertrophied and often conspicuously coloured male-type claw. The necessity for such advertisement is enhanced in carnivorous forms in which the male, if he does not advertise the existence of a sexual situation, is likely to be regarded by the female as an object in the more normal food-situation. This is the case in spiders (see Bristowe [3]). In the hunting spiders with good eyes the display is visual, in the web-spinners tactile (vibration of the web in a special way). However, just as in the deep sea two opposed adaptations to dim light are found side by side, great enlargement and total reduction of eyes, so here an

alternative method is to endeavour to escape the female's notice altogether while approaching. This occurs in the cryptic sexual behaviour of male mantids ('negative courtship'), and is perhaps correlated with overpowering carnivorous propensities in the female (see Roeder [47]).

A peculiar device is that of the presentation of food to the female. In some of the carnivorous *Empidae* this takes the form of actual prey, but in certain vegetable feeders (e.g. the tree-crickets, *Oecanthus*) the male secretes a nutritive sweet juice from a special gland. This, as Richards stresses, is probably correlated with the need for extra nourishment for the maturation of the ova, such as we know exists in, e.g. mosquitoes, and if so, will have an advantage in regard to efficiency of reproduction as well as in securing fertilization; in *Oecanthus* it undoubtedly also serves to distract the female's attention from the spermatophore of which she eats the remains when the sexes separate. In the Empids it appears also to be correlated with the need for immobilizing the female in the proper position for coition to occur.

How easily one type of epigamic mechanism grades into another is shown by the fact that, in other *Empidae*, a conspicuous balloon of specially-secreted bubbles is carried by the male; into this is inserted in some cases the prey, in others a bright object such as a flower-petal. In some species of *Hilara* the female goes through the motions of eating even in the absence of food. This ritualization, as Richards points out, is probably correlated with a rigid chain-reflex type of behaviour. The ritual preening, &c., of some birds during display (Huxley [18]) must have some other origin. Possibly the ritualized actions provided the evolutionary basis of the display.

Finally, we come to combat. This is not employed to any great extent on this level. At this stage, to find the female or to stimulate her readiness to coition will usually suffice; failing this, the expedient of carrying her about, which would be impossible with the more elaborately organized terrestrial animals of the next higher level, can be adopted. There may be some rough-and-tumble rivalry preparatory to seizing the female in some forms, such as frogs, and probably in various insects; but highly developed masculine weapons, as in stag-beetles, are rare, and the evidence that the allometric weapons of male

beetles are actually much used in combat is not strong. The chief exceptions are forms in which some kind of territorial system is developed. These comprise various fish (e.g. stickle-back, paradise fish), in which the male guards the nestful of eggs, and his bright colours appear to be mainly or solely concerned with threat to rivals; and lizards (see Noble and Bradley [40], Evans [6], Kramer [27]) in which no courtship-display exists, the female being either entirely passive in regard to coition, or else having to be subdued by force or by special soothing organs; and the males' bright colours are entirely directed against trespassers and rivals of the same sex. Painting over the colours on a male lizard causes him to be treated as a female, and vice versa for females with male colours painted on (Noble and Bradley [40]).

An apparent exception to the rule of rarity of combat at this level is its prevalence in various polygamous birds and mammals without association of the sexes for other functions than coition (sea-elephant, ruff, blackcock, &c.). Such cases, however, certainly represent a secondary condition, developed from one involving some form of family. Here we may draw attention to the fact that the relative size of the sexes appears to have little to do with any fundamental metabolic difference, but to be correlated with the sexual biology of the species. Where male parasitism is involved, the male is very much inferior in size; and where pursuit occurs, he is rather smaller; where male combat is the rule, the males tend to be larger, but where both sexes fight, the difference in size is small. Certain puzzling cases (e.g. the large size of female Accipitres) remain; but, in general, these correlations seem to hold.

When we come to the final or family stage, matters become more complex, first because there is greater complexity in the form of the association between the sexes, and, secondly, because the animals concerned are at a higher level of nervous organization and behaviour. The securing of a mate no longer implies the securing of coition, for pairing-up may be for life, and even when for the season or brood only, often occurs some time before the female is physiologically ready for coition. Further, the type of psycho-physiological organization found in, e.g., birds, makes it possible, as we have seen, for display and rivalry to have an effect on reproductive efficiency as well as on readi-

ness for coition. This same fact in many cases makes it advantageous to intensify the stimulative effect of display and rivalry on reproductive functions by means of social epigamic gatherings (see above).

Finally, the existence of family duties undertaken more or less equally (grebes, herons, divers, &c.), or in part (most small birds) by the male as well as the female, introduces new complications. The evolution in the male of such essentially female instincts as brooding or feeding the young tends to be reflected in a greater similarity of the sexes in other respects, leading to partial or complete mutual display, with the evolution of appropriate epigamic colours and structures by both sexes. And the importance of family life will mean that advantage to the species may be secured by extending mutual display throughout the breeding season (grebes, egrets, &c.), apparently to serve as a bond between the mated pair (Huxley [19], Southern [51]).

Some insects presumably come into this category, but their epigamic behaviour is not sufficiently well known to permit discussion. Otherwise, only the mammals and the birds appear to be included.

In mammals other than higher primates reproduction is more automatic and physiological, more largely under the control of lower nervous centres, while in birds, as we have seen, it is more related to emotional states and more under the control of higher nervous centres, with the result that stimulative display is rare in the former, common in the latter.

Sexual and Natural Selection

We must now discuss the desirability of marking off sexual selection sharply from natural selection and the relation of male secondary sexual characters subserving combat and display to other characters, found in one or both sexes, concerned with fertilization and other aspects of reproduction.

It will be better to take the latter point first. By now it should have become clear that there is nothing unique or even distinctive about either the nature or the evolutionary origin of male secondary sexual characters concerned with combat or display.

In the first place, display and rivalry are often intimately associated, one being in a sense the obverse of the other, with

the same characters employed (though usually in slightly different ways or with different relative emphasis) for both functions, and often for sex-recognition as well.

Next we come to the sex-limited nature of the characters dealt with by Darwin. Even in some species if weapons exist which are exclusively used for combat with rivals, this condition grades insensibly into that where the weapons are of use in the general struggle for existence by being employed against enemies of other species, and then passes over into that where the weapons are developed in varying degrees of completeness in the female also. Furthermore, sexual rivalry and combat among females as well as males may exist, notably in territorial passerine birds, and not merely in cases of 'reversed sexual selection'.

Nor are display and associated characters confined to one sex, but all gradations exist up to equal elaboration in both sexes. Thus characters concerned with display, rivalry, and combat are not confined to one sex only, though they are, of course, more frequent in the male.

Nor can it be said that, even when sex-limited, they only promote the success of one male as against another. We have just noted that male weapons may be of service in the general struggle for existence. Similarly, display, threat, and combat may also be of general advantage in securing the union of the gametes or even in promoting more efficient reproduction.

Further, such characters grade quite insensibly into those universally considered as of general advantage to the species—the accessory and the primary sex characters. Combat grades into prehension. Then, as Darwin himself noted, organs of prehension do not fall readily into either category; from one aspect they are the product of intra-sexual selection, from another merely organs for securing efficiency in mating.[1] They further grade completely into copulatory organs.

As regards display-characters, Darwin related their origin to female choice. We can now see this aspect of the question in broader perspective. True choice in any psychological sense, or even in the objective sense of the realization of one or two or more alternatives in the way of potential mates, appears

[1] See Richards [46] for further discussion.

to be rare. Darwin, however, had touched on an important principle. Female choice was, for him, part of the selective mechanism involved in the origin of male display characters. If we reject the word *choice* and substitute *sense-organs and higher nervous centres*, the statement is correct. Darwin was the first to state explicitly that the senses and mind (higher nervous centres) of another organism must be part of the selective sieve for certain types of characters. For such characters I have suggested the general term *allaesthetic* (Huxley [21]). If we consider from this angle the characters whose origin is supposed to be due to sexual selection, we shall again find that they grade off into other types of characters.

Display-characters are, as we have seen, inextricably entangled with those subserving threat and also sex-recognition. Threat to rivals passes insensibly into warning to enemies, and the two are often combined. Similarly, sex-recognition may be combined with recognition of other types. Deflexion may be combined with distance threat or with recognition.

The chief interest of such characters appears to me to be the light they throw on the sensory and cerebral capacities of organisms. It is no coincidence that mammals (apart from primates) are restricted to a narrow range of coloration; the fact is correlated with their lack of colour-vision. The type of pattern employed in pure threat, pure display, &c., throws valuable light on the psychological processes of lower organisms, and helps to demonstrate their essential similarity to our own. The majority of allaesthetic characters in higher animals appear to be concerned with mating and reproduction; and the study of such characters and their mode of employment does throw valuable light on comparative psychology and demonstrates that psychical or allaesthetic selection has been at work in their evolution.

It will be as well to summarize in tabular form (see Table 1, next page) the relation of the characters that Darwin considered to be due to sexual selection, to the two more general categories of epigamic and allaesthetic characters.

We must, finally, discuss the selective implications of the facts. It is clear that Darwin's original contention will not hold. Many of the characters which he considered to owe their evolution to sexual selection do have value to the species in the

general struggle for existence, and not merely in the struggle between males for reproduction. Broadly speaking, sexual selection is merely an aspect of natural selection, which owes

TABLE I. *Epigamic and allaesthetic characters in relation to Darwin's theory of sexual selection*

Group	Character	Darwin
Allaesthetic	A. Cryptic	Considered by Darwin as due to natural selection. . . .
Allaesthetic	B. Conspicuous (Sematic): Mimicry, Warning, Deflexion, Recognition	Considered by Darwin as due to natural selection. . . .
Allaesthetic and Epigamic	Sex-recognition	natural selection / sexual selection
Allaesthetic and Epigamic	Display, Threat, Combat	. . . as due to sexual selection. . . .
Epigamic	Prehensile organs	sexual selection / natural selection
Epigamic	Copulatory organs, Other accessory and primary sex-characters, Gamete-characters	. . . as due to natural selection.

its peculiarities to the fact that it is concerned with characters which subserve mating (epigamic characters), are usually sex-limited, and are often of allaesthetic type.

If we wish to employ a special term for this aspect of selection, it will be better to drop the phrase sexual selection, since it has so many false connotations, and substitute *epigamic selection*.

In certain cases, however, Darwin's original contention does hold, and there is a struggle among males for reproduction, success in which is very largely (though probably never wholly) irrelevant to success of the species in the general struggle for existence; this occurs e.g. in certain polygamous birds and mammals (ruff, sea-elephant: see references in Huxley [19]). In other cases there is also a struggle between males, but success in this may be bound up with the general welfare of the species; this is so, e.g. with stimulative display and threat in monogamous birds.

Two points of principle, both of them of great general interest, are thus involved—first, the existence of a sex-limited

form of intra-specific selection (intra-sexual selection); and secondly, the degree to which the results of intra-sexual selection may be divorced from general utility to the species. Neither male preponderance nor polygamy is, as Darwin supposed, necessary to bring about intra-sexual selection.

Intra-sexual selection will always exist when some members of a species remain unmated or fail to effect fertilization efficiently. In territorial birds, those males which do not arrive early on the breeding-grounds, stake out their claim promptly, advertise it, and defend it vigorously over the considerable period till incubation begins, may find themselves relegated to the considerable group (in most passerines apparently comprising 20 to 30 per cent. of the adult population) of non-breeders, without a mate. Further, even should a male secure a mate, his display must be up to the mark, if the number of young he fathers is not to fall below normal.

In all these respects, selection, even in the absence of female choice, is intra-sexual. But—and this is a point not always clearly grasped—it is also promoting the general welfare of the species. In this particular case, of monogamous passerines, the evolutionary mechanism by which effective reproduction is secured automatically involves intra-sexual selection; the struggle for existence of the species is bound up with the inter-individual struggle for reproduction among the males. This is a frequent phenomenon; inter-specific advantage, e.g. as regards efficient feeding mechanisms, may be brought about primarily by intra-specific struggle. In general, there are very few selective situations in which an intra-specific component of some degree is not involved.

But intra-specific struggle, even though it may happen to be the main selective component in the mechanism for promoting general advantage, may have certain characteristic results, notably in pushing adaptation beyond the point at which it is of advantage to the species, and causing hypertely. The degree to which it brings about this result will depend on the intensity of the intra-specific selective advantage, balanced against opposing advantages in competing or incompatible characters. The most obvious balance of this sort in the phenomena we are discussing is that between protection (through concealment) on the one hand, and recognition, threat,

or display (through conspicuousness), on the other. Where there is great selective pressure for concealment, as in small ground-living birds of the open country, it overrides other considerations, and conspicuous characters are reduced to a minimum; when the reverse is the case, as in large gregarious birds like egrets or spoonbills, the coloration may be wholly conspicuous.

In intra-sexual selection the quantitative relation of the purely intra-sexual advantage enjoyed by successful males, to the general advantage of the species, may vary enormously.

In the first place, we have the *fractional* advantage involved in full as against incomplete reproductive efficiency. This, for instance, would operate in regard to the effectiveness of display in monogamous passerine birds, in which display is not related to securing a mate, but to coition and reproduction after mating-up. One male may be slightly less efficient than another; but the upper limit is set by the normal reproductive capacity of a single female, so that the advantage enjoyed by one male over another in the inter-sexual struggle is merely a fraction of this unity.

Doubtless in correlation with this low intensity of advantage we find that display-characters in monogamous territorial passerines are never very strongly developed (see, e.g., Howard [14]). Further, the purely intra-sexual advantage coincides almost entirely with general advantage, so that characters useless to the species have not been evolved.

Next we come to what we may call the *all-or-nothing* advantage involved in securing or not securing a mate. Two very distinct divisions of this exist, the first (*unitary*) when the greatest advantage is the securing of a single mate, the second (*multiple*) when it is the securing of several mates.

Unitary mating advantage is most obviously present in cases of true monogamy when members of a pair stay together for the period of reproduction (brood, season, or life). It will also operate in all cases of one-to-one mating, where the fact of a male's success with one mate precludes him more or less completely from securing a second during the same reproductive period. This appears to hold for at least the great majority of arthropods, molluscs, and lower vertebrates in which mating association occurs. Characters subject to this type of selection will therefore include all those involved in securing mates on

TABLE 2. *Advantages secured by epigamic characters at different levels of reproductive organization*

(Letters denote alternatives; numbers denote conditions that may be combined. Advantages *in italics.*)

(A) Forms without mating, i.e. with liberation of gametes without reference to a single individual of opposite sex.	
(*a*) Without social gatherings for liberation of gametes. *Obtaining synchronous liberation of gametes.*	
(α) by adaptation to environmental factors:	forms with lunar periodicity in reproduction.
(β) by chemical stimulation:	sea urchins, &c.
(*b*) With social gatherings for liberation of gametes:	some polychaete worms.
1. *obtaining synchronous gatherings*: by adaptation to environmental factors:	
2. *obtaining synchronous liberation of gametes*: by mutual stimulation:	
(B) Forms with mating: i.e. with association of two individuals of opposite sex, but in relation to coition only.	
(*a*) *Obtaining mating with one mate*:	
(α) by olfactory discovery:	oak-eggar and other moths.
(β) by visual discovery:	glow-worms, fire-flies.
(γ) by auditory discovery:	frogs, toads, crickets, grasshoppers.
(δ) by continued prehension:	amphipods, some crabs, anura.
(ε) by tactile stimulation:	pulmonata.
(ζ) by advertisement display (of a sexual situation):	fiddler-crabs, spiders.
(η) by stimulative display:	newts, some *Empidae*, *Drosophila;* scent-organs of butterflies and *Hepialus*.
(θ) by presentation of food:	some *Empidae*.
(ι) by combat or threat:	stag-beetles, lizards, sticklebacks, fighting-fish.
(κ) by concealment:	mantids.
(λ) by pursuit:	social hymenoptera.
(*b*) *Obtaining matings with more than one mate*:	
(α) by combat:	sea-elephant.
(β) by display:	? birds of paradise.
(γ) by combined combat and display:	ruff, blackcock. ? birds of paradise.

(C) Forms with association of the sexes protracted, and in relation to other functions than coition:	
1. *Obtaining a mate or mates*:	
(*a*) *obtaining a single mate*:	
(α) combat:	most monogamous mammals.
(β) combat combined with advertisement or rivalry:	most territorial and other monogamous birds.
(*b*) *obtaining more than one mate*:	
(α) combat:	deer, various primates.
(β) combat combined with sexual advertisement:	? various gallinaceous birds.
2. *Securing coition*:	
(*a*) via lower nervous activity (physiological methods):	most mammals.
(*b*) via higher nervous activity (psycho-physiological methods) display usually combined with threat and rivalry:	
(α) non-social:	most birds.
(β) social (cumulative):	some birds.
3. *Securing full reproductive efficiency* (normally combined with (2 (*b*)):	
(*a*) via reproductive physiology: display usually combined with threat and rivalry:	many birds (ruffed grouse; probably most passerines).
(*b*) via family organization (additional to (3 (*a*)): Mutual display:	great crested grebe, herons, &c.

our highest level of organization and most of those involved in securing mating on our second level. The greater the percentage of individuals which do not succeed in breeding, the higher the intensity with which it acts. As between those individuals which do and those which do not succeed in breeding the differential advantage is all-or-nothing; but an upper limit is set by the maximum reproductive capacity of a single female.

In so far as earlier success in mating is correlated with greater vigour of mates secured, or with greater reproductive capacity owing to better utilization of the available breeding season (see Darwin [5]; Fisher [8]), a fractional advantage will also accrue to the possessors of the most successful weapons or epigamic characters.

That the intensity of selection may be high in such cases may be deduced from the elaboration of certain characters developed in relation to it, e.g. the antennae of male bombycid moths, the

jaws of male stag-beetles, &c. Where territorial systems of any sort are in operation, the intensity of intra-sexual selection will tend to be high, since usually a larger proportion of individuals will fail to breed. Epigamic characters and weapons concerned with territory then tend to be strikingly developed, e.g. instincts and colour of male sticklebacks; song, pugnacity, and distance threat characters of many birds; in the latter instance the greater development of such characters than of those (like display characters) associated with fractional advantage is often marked. For the same reason, the hypertely of such characters is often evident. The unwearied singing and territorial flights of territorial birds, the size of male weapons in various beetles, or the display claw of male fiddler-crabs are examples; and we have already cited the earliness of arrival on their territories of males of many birds as a character which would appear to be more or less useless to the species.

Finally, we come to multiple advantage. This only occurs in relation to a disturbance of effective sex-ratio, usually by polygamy *sensu stricto*, or by promiscuity, so that the advantage of success may be to multiply the male's ability to have descendants by several units of female reproductive capacity, while, at the same time, the percentage of non-breeding males in any one season is much increased, usually to over 50 per cent. and sometimes to a much higher figure.

This being the case, the possible purely intra-sexual advantage can be very much higher relative to general benefit to the species; and, accordingly, we here (and here alone, so far as I am aware, in the field of sexual characters) find the development of characters that must be deleterious to their possessors in the general struggle for existence. The train of the peacock and the tail of the Argus pheasant are often-quoted examples. Hypertely is correspondingly frequent. The display-plumes of male birds of paradise and the immense size of the male sea-elephant are illustrations. In general, male characters subserving combat and display are often pushed to the mechanical limit of possibility.

Four types of polygamy occur. There is first polygamy proper, in which a family life exists, the successful male accompanying a number of female and young individuals of both sexes; this occurs in baboons (where the male is the dominant

leader of the group), in deer (where the group-leader is a female: Darling [4a]), in various other mammals, and apparently in certain pheasants and other gallinaceous birds. In the second place, there is promiscuity, in which not only is there no family association between the sexes, but a male will mate with more than one female and apparently a female with more than one male. This occurs only in birds, presumably because of the less importance of male combat and the greater importance of emotional stimulation and is always associated with social display at special spots. At these gatherings, emotional excitement among the males is intense, and the two facets of sexual emotion, rivalry and display, are always combined. Examples are ruff, blackcock, and probably various birds of paradise.

It appears definite that true female choice, of the type postulated by Darwin, in which a female deliberately selects one male from among a number of rivals present at one time, does occur in such cases; but there is little evidence of its occurrence in other circumstances.

Thirdly, we have territorial polygamy (p. 25), which is a specialized development of the territorial system in passerine birds, and fourthly, there is mating polygamy, which is in a sense intermediate between the first two. It occurs when association between the sexes occurs for some time, but is related only to mating, not to any other aspect of reproduction. It is the simple harem system, uncomplicated for the male by family responsibilities. Its best development is in the sea-elephant and other fur-seals. As promiscuity is an outgrowth of the avian type of reproductive organization, based on emotional stimulation, so mating polygamy is an outgrowth of the mammalian type, based on male strength and the possession of a troop of relatively passive females. It is a specialization of true (family) polygamy, not of social display and mating; but though so different in origin, its quantitative selective consequences are the same.

Probably in no other sphere can the relative shares of general advantage and purely individual advantage in intra-specific selection be so clearly evaluated as in intra-sexual selection; this is because the advantage of individual males is sharply separable into grades owing to the fact that it often operates

in an all-or-nothing way, by the addition or subtraction of whole units of female reproductive capacity.

To sum up, intra-sexual selection is inevitably part of the mechanism by which mating efficiency is evolved and maintained. In many cases individual and general (species) advantages coincide. With increasing intensity of selection between males, epigamic characters that are hypertelic or even useless to the species are developed, and with polygamy such characters may be evolved to the limits of mechanical possibility, and even be disadvantageous to their possessors in all respects save that of mating.

Even if we drop the term sexual selection, we must agree that the topics discussed by Darwin under this head, which we must to-day deal with in relation to the overlapping concepts of epigamic, intra-sexual, and allaesthetic selection, were of peculiar nature and fundamental importance, and that to have linked them together by means of a single theory was of great value in the history of biological thought.

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THE GENETIC BASIS OF ADAPTATION

By E. B. FORD

GENETICS, being a subject of recent development, is not only growing rapidly but changing. It is valuable, therefore, to pause now and then and review the position which some of its concepts have reached. The present occasion provides an opportunity for doing so. It may be used briefly to survey a few aspects of variation, with special reference to selection and, in particular, to the evolution of adaptations.

At the outset, it is well to establish once more certain fundamental principles. The investigations of Johannsen on pure-lines in beans, often confirmed on other material, have proved experimentally a logically evident fact: that selection cannot modify a population however diversified, unless the variations subjected to 'choice' are inherited. The nature of the inheritance involved therefore becomes a matter of primary importance. Its analysis is simplified by the fact that the number of ways in which it can possibly be controlled are limited to a few main types.

Theoretically, the hereditary factors, transmitted by the gametes, may be carried either in the nucleus or in the cytoplasm. Now the amount of nuclear material received from the two parents is equal, while, in higher forms at any rate, their cytoplasmic contribution is exceedingly dissimilar. We may obtain the two correlation coefficients between the variation of a given character in a number of offspring and in their male and female parental groups respectively. Their substantial equality indicates that no significant proportion of the heredity involved is due to cytoplasmic transmission. Though such a basis is not actually unknown, it proves to be exceptional: a conclusion which is evidently susceptible of the widest verification.

Seeing then that the vast majority of the hereditary factors are carried in the nucleus, two distinct possibilities arise. Either the contrasted types retain their identity, or else they blend with one another when united in the same individual. In the former situation, recombination will cause the second inbred generation to

be more variable than the first. In the latter, however, such a condition appears to be excluded; for blending must tend to uniformity. Even if the variability were to be maintained by constant changes in the factors themselves (that is to say, by a high mutation rate), sufficient to counterbalance its rapid decay, the second hybrid generation would not be the *more* variable: we have no ground for supposing that in a constant environment mutation will affect successive generations unequally. The universal tendency for the grandchildren to be more variable than the children, when produced by inbreeding from individuals exhibiting contrasted characters, assures us that heredity is in the main controlled by the particulate, or Mendelian, mechanism.

Mutation must be defined as a change in any unit of heredity. Now such changes would have to occur with great frequency if they were successfully to oppose the results of blending. Actually they prove to be very rare: no more numerous in fact than is necessary to maintain genetic variability on the assumption, already reached, that the individuality of the factors is preserved. These considerations have been developed with much skill by Fisher [4]. They show that the mechanism of evolution must be analysed on the understanding that mutation very seldom takes place. Indeed, an approximate rate of 1 in 10^5 seems to approach the upper limit for its occurrence at any one locus, while 1 in 10^6 may be regarded as a more usual level.

Genetic factors have multiple effects, and they interact with one another to produce the characters for which they are responsible. The chances, therefore, that any random mutation shall upset rather than improve the adjustment of the organism to its environment are very great. However, a gene having beneficial effects will be produced now and then. It will be spread through the population by selection, until its former normal allelomorph has become a rarity: favourable forms will not long remain 'varieties'. Consequently, if the mutations which we encounter in genetic work really represent the type of change used in evolutionary progress, we should expect their results almost always to be disadvantageous, as in fact we find they are.

It seems that such 'mutant genes' are generally pressed into the recessive state by selection operating against their hetero-

zygous effects (Fisher [5]). That normal individuals carry them in numbers is now well known: so, too, is the reality of the selective influence brought to bear upon them. For example, by breeding as far as the F_2 generation, Gordon [10] was able to obtain at least 14 genes, recessive in operation, from 23 wild females of *Drosophila melanogaster*, and 22 from 16 females of *D. subobscura*. Of these, only two were sex-linked, while no further sex-linked recessives appeared by raising the F_1 generation from an additional 35 wild *D. melanogaster* and 81 *D. subobscura*. Now the proportion of genes showing sex-linkage should correspond with the ratio of the length of an *X*-chromosome compared with the sum of the lengths of each type of autosome (excluding inert regions). Judged on this basis, it is clear that sex-linked recessives are deficient in both these species. The influence of selection is here evident. Those genes are eliminated more rigorously whose disadvantageous effects are invariably expressed in half the population than are those in which they are masked save as rare homozygotes (Gordon [11]).

We may reasonably anticipate that genes responsible for minute advantages are constantly spreading in the population, displacing their allelomorphs, and adapting their possessors more perfectly to their environment. The greater variability of abundant as compared with rare species, apprehended by Darwin, provides evidence for this conclusion.

Suppose an advantageous mutation of any kind occurs in one individual in 10^7. If this number only breed, the new gene is quite likely to be lost by random extinction, but less likely if 10^8 breed. Furthermore, it can be shown (Fisher [3]) that mutations producing genes of nearly neutral survival value must be excessively rare. Nor can we suppose that they occur with different absolute rates in common and scarce species. Fisher [6] has therefore pointed out that the number of these 'neutral genes' which any species can maintain will be nearly proportional to the logarithm of its population. That is to say, when very rare, their existence will favour but little the variance of the commoner forms which, however, can keep more of such genes in reserve. Changes in the environment may from time to time cause the effects of any of them to become slightly advantageous. The gene in question will then spread, giving rise to increased variability, reaching a maximum when it and

its allelomorph are present in the population in equal numbers. Consequently, any observable difference in variability, when ascribable to the population level of the species concerned, will be due to the spread of advantageous genes actually engaged in bringing about evolutionary change. Such comparisons are laborious and not easily made. However, two sets of observations have now demonstrated that abundant species are more variable than rare ones. In the first, the colour-variation of a group of night-flying moths was related to the abundance of the species (Fisher and Ford [7]); while in the second, egg-size in birds was selected for similar treatment (Fisher [6]). The data so obtained demonstrate the existence and spread of genes giving rise to small advantageous effects in natural conditions.

It has already been pointed out that the influence of a gene may be disadvantageous in one environment and advantageous in another. It is worth while to reflect upon the adjustment of an organism to its surroundings from this point of view. Any form will endeavour to secure optimum conditions, and in these it will remain so far as possible. There is a tendency, therefore, for all species to live in a constant environment, being that which suits them best. This is the one in which they are selected, and in which the effects of the genes are usually judged. In it, too, the gene-complex is balanced so as to enhance favourable qualities and to minimize undesirable ones. The chances are very small that any random change shall prove beneficial in circumstances such as these. As the optimum is left, two components have to be considered. First, the species finds itself in a situation to which it is not properly adapted, and secondly it may not retain its former characters unmodified, for the genes may interact with their fresh surroundings in new ways. The possibility of a random change being useful is a little greater now: still more so when lethal conditions are approached.

It would appear to be an ideal system, therefore, for organisms to vary less in their optimum environment than in any other. There are indications that such an arrangement is sometimes actually realized.

An example of it seems to be provided by certain of the instances in which asexual and sexual methods of reproduction may succeed one another in the Protozoa. For example, it

is well known that the asexual type is usually employed by *Paramecium*, the individuals generally dividing by binary fission so long as the culture conditions remain good. In these circumstances, genetic variation is largely restricted to mutation. As the supply of suitable food becomes exhausted and waste products accumulate, conjugation, which normally occurs sporadically, takes place more frequently. It has been shown that this gives rise to a great outburst of genetic variation (Jennings [15]). Most of the forms produced are less well adapted to the environment than was the original clone. Many, indeed, are visibly deformed, and the majority perish in the intense selection to which they are subjected. On the other hand, this preserves those which can withstand the conditions best, and a temporary improvement in the viability of the stock often takes place. However, a steady deterioration in the culture will of course ultimately lead to an environment which the species is quite unable to tolerate.[1]

In examples such as these we find that variation is reduced when conditions are favourable, for then it will almost certainly lead to nothing but wastage. When they depart from the optimum the organism varies more, by undertaking a greater amount of sexual reproduction. The advantage of doing so at that time is apparent from the improvement which sometimes results. The work of Beers [1] on the Ciliate *Didinium nasutum* illustrates very clearly this aspect of the subject. He found that conjugation led to increased vitality in stocks which were in a state of decline, due to under-feeding.

It is interesting to consider how far such a tendency is traceable in higher forms. It may be that it is to be detected in those plants which have a great capacity for asexual reproduction and resort but rarely to the sexual method. So, too, it is apparent in the occurrence and distribution of parthenogenesis and apogamy. Structurally, these may appear to represent intermediate steps between the asexual and sexual

[1] Probably the advantage of endomixis is largely concerned with the renewal of the macronucleus, in which waste products may accumulate. Parker [17] has, however, shown that the process leads to genetic variation in *Paramecium aurelia*. As this species possesses two micronuclei, endomixis may here give opportunities for recombination in a manner from which it is not justifiable to generalize. In any event, its occurrence does not obscure the effect of conjugation in promoting variation as conditions become unfavourable.

methods of reproduction, but they do not in fact indicate such a transition. Rather, they have been imposed secondarily upon the sexual type. This is indicated by the frequent existence in such forms of traces of chromosome reduction, to be overcome by a number of devices which have evidently been independently acquired. For it is of course essential that the chromosomes should be reduced to the haploid number in the gametes of sexually reproducing species, and equally essential that they should remain diploid in those which are parthenogenetic (unless facultatively so). Nor are the latter to be found among primitive organisms, but rather among the highly adapted types so closely adjusted to their environment that their variation is exceedingly likely to be disadvantageous.

Now, as any evolving line becomes more highly specialized, the variations which could possibly be of use to it are progressively restricted. Finally, it attains a state of 'orthogenesis', in which the only changes open to the species are those which push it further along the path which it has already pursued. Evolution of this kind is very common, and it must necessarily lead to extinction; for it is impossible for such forms to adapt themselves in new ways to suit changes in the environment. Their last phase, when almost all variation is bound to be dangerous, should, where practicable, be accompanied by parthenogenesis.

In such circumstances, the process is of rather gloomy significance. When combined with the sexual method, however, it may give rise to very satisfactory results, as it seems to do in many insects. These are akin to the alternation of asexual and sexual reproduction in the Protozoa. As pointed out by Snell [22], facultative parthenogenesis combined with haploidy is to be regarded as a eugenic measure of a rather special kind. Thus in the honey-bee, all recessive characters are expressed in the males, which arise from haploid eggs: a fact of course uninfluenced by the subsequent chromosome doubling which occurs in the majority of their tissues. Selection will therefore purge the species of genes having disadvantageous effects: while the competitive nuptual flight must make the process an especially rigorous one.

We may well look for further evidence of the greater variability of species as they depart from their optimum. It is not

impossible that a circumstance at present little investigated may prove to be an example of this tendency. It is clear that, in the widest sense, the effect of crossing-over is to increase the variability of the organism. Were complete linkage to exist, genes in the same chromosome would have to compete with one another in the same way that the members of a multiple allelomorph series in fact have to do. Now the cross-over value of a few regions of the chromosomes of *Drosophila melanogaster* has been studied over the range of temperature which the species will tolerate. When the results so obtained are examined, it is found that they include two apparently distinct conditions (Graubard [13]) which, however, may well differ only in degree. In those segments which are far from the attachment constriction, the value does not alter, at any rate to an extent which has so far been detected. In those nearer to it, however, crossing-over varies with the temperature in a peculiar way. The cross-over value is high in cool and in hot conditions, and low in intermediate ones (Plough [18]). That is to say, when plotted against temperature as the abscissa, the curve obtained is U-shaped. However, it has a flat base, as a fairly constant low level is reached over the range 22°–27° C. There is a slight falling off in the value at the ends of the U beyond the two maxima of 13° and 32° C. respectively. This is, perhaps, only doubtfully significant as these extremes are nearly lethal. Now it is to me a striking fact that the range of lowest cross-over values includes the optimum temperature for this fly (23°–25° C.). It has, of course, been pointed out that the shape of the curve resembles that obtained for the contraction of frog's muscle at varying temperatures, and a mechanical interpretation has therefore been placed upon it. The fact remains that, directly or indirectly, the cross-over value in certain regions is so adjusted as to reduce variability at the optimum, and to increase it as the temperature departs therefrom in either direction.

The number of instances in which the cross-over value has been obtained over such a wide range is, unfortunately, very small. It has several times been observed that it increases when the environment becomes warmer than normal (Eloff [2]), but it has been very little studied in the cooler conditions which the organism will tolerate. It would be valuable to obtain data on this subject for a number of different forms.

If, as I am inclined to suspect, selection has been responsible for the reduction of crossing-over at normal temperatures, the type of variation necessary for it to act upon would certainly seem available. Many genes are known which affect the cross-over value of *Drosophila melanogaster*: from the extreme condition of one in the third chromosome which entirely inhibits it even in the female (Gowen [12]), to those modifying it to a small extent in their own neighbourhood only (Serebrovsky, *et al.* [21]). Seeing how susceptible are the effects of the genes to changes in the environment, it is highly probable that the influence of some of these varies with the temperature.

Here an obvious question will be asked. Assuming the justice of what has just been said, why should the effect be restricted to (or greater in) certain regions of the chromosomes? It may be that we are here faced by a consideration of the widest significance: that the evolution of any organism is at the mercy of its own developmental mechanics.

Where, for example, sex is under the control of a number of genes, it becomes necessary to suppress most of the crossing-over between the *X*- and the *Y*-chromosomes. It is quite unnecessary, even undesirable, that such suppression should be extended to the autosomes, yet they are very commonly involved in it. Indeed, it is generally true that crossing-over *as a whole* is rarer in the heterogametic than in the homogametic sex; while it may be almost absent in the latter, as in the male of *Drosophila melanogaster*. Had genes been available which so acted as to prevent crossing-over between the required regions of *X* and *Y* only, no doubt they would have been employed; but it seems that most of them have some effect on the autosomes also, and such material as existed has had to be used. So, too, suitable genes may not be available to reduce crossing-over in optimum conditions throughout the length of the chromosomes.

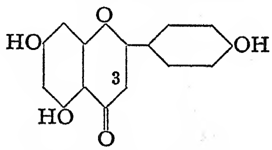
The concept that the evolution of any form must be largely dictated by its own physiological processes deserves some further attention. Evidently it must be important whether or not there exist genes capable of altering the growth-rate of particular organs or the size of the body as a whole, as Huxley's analysis of allometry so clearly shows [14]. So, too, we find that allied species may attain corresponding ends by different chemical means, a fact which may well determine the

adaptations available to them. Furthermore, a gene conferring some potential advantage may or may not be usable according to the way in which it chances in addition to modify the physiology of the organism. It is worth while to quote examples of these two last propositions. We may select one illustrating each from the Lepidoptera.

The large genus *Papilio*, consisting of the swallow-tail butterflies, has an almost world-wide distribution. It is divided into three sections. The first of these, *Pharmacophagus*, comprises those poisonous and distasteful forms which feed on Aristolochia. They act as models for many species, including a number belonging to the two other sections of their own genus. These are the 'fluted swallow-tails', *Papilio* (*sensu stricto*), and the 'kite swallow-tails', *Cosmodesmus*. They are not protected by nauseous qualities, and provide well-known examples of mimicry.

Now I find that the white and yellow colours of the genus as a whole are produced in two distinct ways. Some are 'pterins': pigments with purine bases. These are manufactured by the organisms themselves, and are chemically allied to uric acid. They include pure white compounds like the leukopterin ($C_{19}H_{19}O_{11}N_{15}$) isolated by Wieland *et al.* [23] from *Pieris brassicae* L. Among other colours to which they may also give rise are various yellow shades, as the sulphur coloured xanthopterin ($C_{19}H_{19}O_7N_{15}$) obtained by Schöpf and Becker [20] from *Gonepteryx rhamni* L.

The second group of whitish and yellow pigments existing in these butterflies is derived from the larval food. It consists of the sap-soluble anthoxanthins, comprising the flavones and flavonols. Their structure is of the type:



flavone[1] (apigenin)

They are responsible for ivory, cream, and yellow flower colours, and are at present little, if at all, altered in the scales of certain Lepidoptera.

[1] The flavonols differ in having the hydrogen at position 3 in the pyrone ring substituted by an hydroxyl.

Now as far as my experience goes, the anthoxanthin pigments of the genus *Papilio* are limited to the *Cosmodesmus* group. The number of species in which I have detected them is given in the following table.

Section of Genus	*'Pterin' pigments*	*Anthoxanthin pigments*	*Both types present*	*Total number of species*
Pharmacophagus . .	28	0	0	28
Papilio (*s.s.*) . .	35	0	0	35
Cosmodesmus . .	4	38	3	45

Distribution of types of white and yellow pigment in species of the genus *Papilio*.

It is interesting to notice that the classification of these insects, originally determined on small structural characters, is supported by the chemistry of their pigment formation. Furthermore, there exists a small genus, *Leptocircus*, evidently closely allied to *Papilio*. In discussing its affinities, Jordan [16] maintained that it had been derived from the *Cosmodesmus* section. The occurrence of anthoxanthin pigment in *Leptocircus curius* F. evidently supports this conclusion, reached on entirely different grounds.

However, the matter which directly concerns the present discussion is the fact that a particular type of pigment formation appears to be restricted to a single section of a genus. Such a condition may well influence the possible adaptations open to its various species. It might, for example, limit the models available for their mimicry: a view for which there is in fact some evidence.

This point requires a short explanation. It has been held by Punnett [19] that the resemblances between model and mimic may be due to the existence of parallel mutations in each: just as we know that the variation in eye-colour from red to white in *Drosophila melanogaster* and in *D. simulans* is due to the same allelomorphs in both species. Such a suggestion, however, appears to be untenable. The resemblances involved in mimicry are generally purely superficial, such as deceive the eye and no more. Indeed, the similar colours and patterns are often produced in entirely different ways. Thus the red pigment present in the mimetic form *romulus* of *Papilio polytes* L. (*Papilio s.s.*) is chemically distinct from that present in *P. hector* L., the *Pharmacophagus* species which it copies (Ford [8]).

However, the 'pterin' and anthoxanthin whites are not really

identical. The latter, indeed, are never wholly free from a slight yellowish tint, and it may be that the distinction here involved is appreciated by the predator which it is sought to deceive. Thus the pale patch on the black fore-wings of *Papilio ariarathes* Esp. is generally yellowish. This is due to a flavone, for the butterfly belongs to the *Cosmodesmus* section. In some of its forms, however, this patch is white, in mimicry of *Pharmacophagus* species such as *Papilio echemon* Hbn. Here the pigment employed is a pterin, like that of the models. The genetics of this situation would be of great interest. It serves to show that the mimicry of a species may be modified by its possession of 'pterin' or anthoxanthin pigments.

The limits which the physiological processes directed by a gene may impose upon its possible spread are illustrated by some of the melanic forms occurring in the Lepidoptera. These are controlled genetically in a variety of ways, but the majority of them are unifactorial. Now it is remarkable that in a number of species the melanic insects prove to be hardier than the normal form, so that they generally exceed expectation in segregating families. Only those do so which behave as dominants or semi-dominants: when recessive, they are, as we should expect, the less viable.

This peculiar situation demands attention. It should be observed that an advantage easily detectable during the course of an ordinary breeding experiment is, from the evolutionary point of view, very considerable. It should cause the gene responsible for it to spread rapidly through the species and displace its allelomorph. Yet such advantageous genes have not done so, although the hardly melanic forms to which they give rise are known to occur as rare varieties in normal circumstances, and occasionally they may be not uncommon in some restricted localities.

It appears to me that all such genes conferring greater viability must in fact have been utilized except when they give rise to some counterbalancing disadvantage, such as excess melanin production may well be. For this destroys the procryptic coloration of the insect. In manufacturing areas, however, where the country-side is blackened by smoke and predators are rare, the black colour may no longer be a drawback. Here, at last, the species are able to make use of

the favourable effects of such genes. These then spread, giving rise to the phenomenon of industrial melanism in the Lepidoptera: the most striking evolutionary change which has ever actually been witnessed.

This view is one which has only recently been advanced (Ford [8]). However, the point of special significance for the present discussion is the existence of genes conferring evident advantages, of which the species have none the less been unable to avail themselves. It may be added that the way in which it has become possible for them to do so when the environment changes is well illustrated by *Boarmia extersaria* Hb. This Geometrid occurs in southern England; but it does not enter any considerable industrial areas in this country, and its black variety (*cornelseni*) is very rare. In Germany its range chances to extend into manufacturing districts. Here the melanic specimens have replaced the normal form, though they have not done so elsewhere in the country.

Even when that rare event, an advantageous mutation, occurs, it seems that the organism may be prevented from incorporating it owing to the nature of its own physiology. However, the check so imposed may be removed not only by internal changes but by alterations in the external environment.

It is clear, therefore, that in summarizing those aspects of adaptation which we have discussed, the relation of environmental to genetic variation is inevitably forced upon the attention. We have seen that genes conferring minute advantages are slowly spreading, and in such a way that the numerically larger species have the greater opportunities for fission. It appears, too, that it will be advantageous for variation to be commoner in unfavourable conditions than at the optimum, and that species have to overcome the handicap imposed by their own developmental processes in adjusting themselves to the environment in the way most suited to them.

Now selection will control the genetic variation to which a species is subject, but its environmental variation must also be adapted to its needs. The changes in external conditions to which a form is liable must not evoke disadvantageous responses from its normal genetic equipment. Yet the only way in which the effects of environmental variation can be controlled by evolution is to adjust the gene-complex of the

organism in relation to them. That is to say, it is in this sense impossible to separate the genetic and environmental components of variation, just as it is impossible to regard any character as purely 'acquired' by the individual or determined solely by heredity. This concept has never been expressed more clearly than by Professor Goodrich himself [9], who says 'No single part or character is completely "acquired", or due to inheritance alone. Every character is the product both of factors of inheritance and of environment, and can only be reproduced when both are present. Characters are due to responses, and have to be made anew at every generation. Only those characters reappear regularly in successive generations which depend for their development on stimuli always present in the normal environment. Others, depending on a new or occasional stimulus, do not reappear in the next generation unless the stimulus is present.' Had the significance of these words been more widely appreciated, genetic and evolutionary discussions would have been freed from many of the misconceptions which still obscure them.

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EMBRYOLOGY AND EVOLUTION

By G. R. DE BEER[1]

THE relations between the studies of individual development and of phylogenetic descent have been peculiar and not without importance from the point of view of progress in biological knowledge generally.

Descriptive embryology had already been established for some decades when the theory of evolution by natural selection made its appearance, and very soon, in their enthusiasm for the great new revelation, biologists were making embryological facts subservient to their evolutionary theories. These activities, based on the crude though evident parallelism between ontogenetic stages and rungs in the phylogenetic ladder, presently resulted in the search for the representatives of past ancestral forms in the developmental stages of present-day organisms.

Thus arose the famous theory of recapitulation: a formulation of the relations between embryology and evolution on the assumption that an ontogenetic series of stages was a recapitulation, an abbreviated and accelerated repetition, of the series of *adult* ancestral forms in the previous phylogenetic history of the organism in question.

As is so often the case with half-truths, this theory of recapitulation, promoted by Haeckel to the status of 'fundamental biogenetic law', enjoyed wide acceptance, and to its credit may be placed the incentive which it gave to the continuance and amplification of embryological studies on an ever-widening range of material. Nevertheless, it must be recognized that the theory of recapitulation contained a fallacy which for two reasons impeded the progress of biological work and thought.

The first of these reasons relates to the inability of the theory of recapitulation to accord an evolutionary significance to embryonic and larval variations. The argument ran thus: ontogeny is a recapitulation of adult ancestral stages, represent-

[1] The writer wishes to acknowledge the helpful criticisms which he has received from Dr. J. S. Huxley, Mr. E. B. Ford, and Mr. P. G. 'Espinasse.

ing the 'palingenetic' features in development; any developmental variation which modifies, obscures, or is substituted for a palingenetic feature, is therefore an exception, a 'caenogenetic' phenomenon devoid of evolutionary significance. All this is based on two assumptions: that developmental stages of a descendant do represent adult ancestral types, and that in phylogenetic descent the evolutionary novelty has always occurred in the adult, and has subsequently been pressed into increasingly early stages of development.

The assumption that developmental stages of a descendant represent adult ancestral types has taken all the longer to disprove because of the facile way in which non-crucial observations have been claimed as evidence in its support. Thus, when the visceral pouches of the mammalian embryo were considered, they were at once held to represent the gill slits of *adult* fish. On the facts as they stand, the only justifiable conclusion is that the visceral pouches of the mammalian embryo represent the visceral pouches of the fish *embryo*, for the resemblance goes no farther. There is a *repetition* of ontogenetic events; that is the germ of truth in the theory of recapitulation. What is not true is the assertion that the repeated ontogenetic features represent adult ancestral characters.

In many cases it can be proved that the developmental history cannot represent the phylogenetic history, for the reason that if the adult ancestor resembled the modern embryo, it could not have been functional. An example will make this clear. In higher vertebrates, the lung develops as a pouch which grows into and branches in a thick layer of surrounding mesenchyme. As Professor Goodrich [17] says, 'the lung, to be an efficient organ of respiration, must from the first have had a thin wall abundantly supplied with a superficial network of blood-vessels, and have become progressively folded and pocketed to form the parenchyma of air-cells in higher forms. Thus the respiratory surface, which is the last to develop in the embryo, must have been present from the first and throughout phylogeny.'

There are indications that many important steps in evolution have resulted from novelties which first manifested themselves in early stages of development of the ancestors. Adult modern man finds the closest resemblance to himself in young

Neanderthal man or in new-born apes; the only invertebrate forms from which the vertebrates may plausibly be derived are larval echinoderms; insects may likewise have been derived from larval myriapod-like forms.

This phenomenon, to which Garstang [12] has given the name 'paedomorphosis', is the very opposite of recapitulation, for instead of the embryonic descendant resembling the adult ancestor, in these cases it is the embryonic or undeveloped ancestor which resembles the adult descendant. The theory of paedomorphosis, as de Beer [6] has explained, is much more fertile in providing possibilities for a logical synthesis of the data of embryology and evolution. Instead of being rejected as caenogenetic exceptions, embryonic and larval variations or persistencies may become the leading features of subsequent evolution. Thus, nothing but a larval variation can have brought about the torsion of gastropod molluscs.

It is clear that, at different levels on the scale of evolution, the time in ontogeny at which certain morphogenetic events are repeated may vary. If corresponding events occur relatively earlier in the descendant than in the ancestor, the case may be described as one of recapitulation; if, on the other hand, the corresponding events are delayed in the descendant, the case is one of anti-recapitulation, or paedomorphosis.

The mechanism, whereby such changes in the time of development of a structure may be brought about, has been revealed by recent investigations in the field of physiological genetics which, since they are closely concerned with the study of ontogenetic development, may legitimately be referred to here. The researches of Goldschmidt [14] and of Ford and Huxley [10] into the rates at which genes exert their effects have established the fact that the quality of certain results of development (such as male structures as contrasted with female structures in *Lymantria*, or the colour of the eyes in *Gammarus*) is controlled by the relative speeds at which processes of differentiation occur. These speeds have been shown to be the expression of quantitative properties of reaction-rate on the part of the genes concerned. Since it is known that different genes may have different rates of activity, and it can be observed that the appearance of the characters which they control may be accelerated or retarded, it is easy to understand how in evolution

the phenomena of recapitulation and anti-recapitulation may have been brought about.

These investigations also throw light on the problem of vestigial organs. Evolution has been characterized not only by the appearance and perfection of new characters, but also by the loss of old ones. Huxley [25] has shown that this loss, or reduction to a vestige, is a simple consequence of a decrease in the growth-rate of the structure concerned; such decrease being itself presumably the result of a decrease in the activity-rate of the controlling genes. In early stages of development, both slow-worm and lizard have limbs, but whereas in the latter these limbs go on developing and growing and are present in the adult, in the former they do not, and the adult is limbless. If, as appears to be the case, the first evolutionary steps in the reduction of a structure are brought about by these decreases in growth-rate and the activity-rates of the genes, the presence of limbs in the slow-worm embryo cannot be regarded as evidence of any recapitulation of ancestral adult characters, but merely as the repetition of embryonic characters.

There are some other phenomena which present the appearance of recapitulation, and to which Needham [32] has drawn attention. Many invertebrates excrete nitrogen in the form of ammonia, fish and amphibia as urea, and (adult) birds as uric acid. Now the embryo bird excretes first ammonia and then, later, urea, before finally excreting uric acid. But the fact that this parallelism exists between these two series is no evidence that it represents a recapitulatory phenomenon. On the contrary, it seems to represent the order and sequence in which biochemical reactions of increasing degrees of complexity can be performed. Both in ontogeny and in phylogeny there is a transition from the simple to the complicated, and the sequence of production of these excretory products may be inevitable. In addition, Needham [33] has pointed out that the production of urea by the chick embryo (by means of the arginine-arginase system) is not identical with that which occurs in fish and amphibia (by the ornithine cycle). At all events, the failure to recognize this principle of parallelism of increasing degrees of complexity was a grave error in the theory of recapitulation.

Meanwhile, it must be noted that embryology, in revealing repetition of ontogenetic features, whether accelerated or

retarded, can provide evidence of affinity between groups of organisms whose adult forms are more markedly different, but cannot with certainty reconstruct adult ancestral types. It must further be remembered, as Woodger [41] has pointed out, that ontogeny is a four-dimensional phenomenon in space and time, and that comparison between 'stages', which are nothing but arbitrarily cut cross-sections through the time-axis, cannot always be expected to yield results of any significance at all. Thus, while the fully formed chondrocrania of trout and cod, or the fully formed bony skulls of newt and frog, are readily comparable, de Beer [7] finds that earlier 'stages' of development of these animals are difficult to compare, because relative differences in order of appearance and speed of development of corresponding structures renders them very dissimilar.

In considering the points of view of von Baer and of Haeckel, this much can be said by way of harmonizing them. As von Baer [2] showed, embryonic forms tend to resemble one another more than they resemble adults and more than adults resemble one another. Now, since the ancestor gave rise to the descendant, it was probably more primitive and less specialized than the descendant. Therefore it is *probable* that the ancestral adult did not depart as much from its embryonic form as the adult form of the descendant departs from its embryo. To this extent, then, the structure of the adult ancestral form may sometimes be *inferred* from that of the developmental stages of the descendant. Against this, however, must be set the possibility of paedomorphosis. For if a descendant is derived from the larval form of an ancestor, the adult form of that ancestor may have been specialized to a lesser or greater extent. In such a case, the resemblance between the young form of the descendant and the young form of the ancestor may convey very little or no information concerning the adult form of that ancestor.

The second and, perhaps, the more important reason for which the theory of recapitulation has impeded the progress of biology is that it has blinded embryologists to the necessity for looking for causal connexions within ontogenetic phenomena. If the series of ancestral forms, or phylogeny, were, as was proclaimed, 'the mechanical cause of ontogeny', there was no incentive to look farther afield for an explanation of development.

Foremost among those who refused to be limited in this manner was Wilhelm His [21]. He saw the necessity for analysing ontogenetic events, form-changes, expansions, adhesions, perforations, &c., into simpler mechanical components to which the causal postulate could be rigorously applied. It is interesting to notice the hostility with which his views were met. Haeckel [18] ridiculed them, and retorted that

'each of these simple ontogenetic processes of unfolding is the result of an extremely complicated series of historical events. It is causally determined by the thousands of phylogenetic changes, by the innumerable hereditary and adaptive alterations, which the ancestors of the organism in question have undergone during the course of millions of years.'

As His [22] himself wofully complained, his contemporaries objected that they had

'better things to do in embryology than to discuss tensions of germinal layers and similar questions, since all embryological explanations must of necessity be of a phylogenetic nature. This opposition to the application of the fundamental principles of science to embryological questions would scarcely be intelligible had it not a dogmatic background. No other explanation of living forms is allowed than heredity, and any which is founded on another must be rejected. The present fashion requires that even the smallest and most indifferent inquiry must be dressed in a phylogenetic costume.'

It is well to realize that this was the prevalent state of mind in order to appreciate the acuteness of His's criticisms and the achievement of Wilhelm Roux in founding the new science of developmental mechanics. This study is usually but perhaps unfortunately referred to in English as 'experimental' embryology, which suggests that the discoveries of descriptive and classical embryology were not investigations into nature. Rather should the introduction of controlled conditions into embryological studies be known as 'analytical' embryology (Weiss). Be that as it may, this work has shown, at the hands notably of Hans Spemann and Ross Harrison, that developing organisms 'make themselves', proceeding from successive internal and environmental causes (many of which are now recognized as chemical and physical) to effects, by means of 'organizers'

which induce differentiations of particular qualities out of reacting tissues, and functional adaptation.

In so far as the past plays any part in the events of ontogeny, it is not phylogeny or the series of adult ancestral forms, but the inherited and undeveloped germ-plasm which imparts to each organism the capacity to respond to certain stimuli in the manner recognized as development from the egg, ensuring that if development occurs at all, it conforms to the type of the species. Development has thus been shown to be an epigenesis of material of which the possible qualities are predetermined.

At the same time it must be remembered that the developing organism, no less than the adult, is subject to the eliminatory action of natural selection, not only as regards essential details of metabolism of all the tissues, but also as regards the retention of structures which perform essential functions. The visceral pouches of an amniote embryo will never be used in the manner in which the visceral pouches of fish embryos will subsequently be used. One reason why amniotes preserve this heritage seems to be because out of the visceral pouches the thymus and parathyroid glands are developed, and these, and therefore indirectly the visceral pouches, are necessary for survival. The notochord in higher vertebrates is no sooner formed than it is destroyed by the vertebral column. It is nevertheless formed, no doubt partly because during gastrulation the cells which later constitute the notochord have the power of organizing and inducing the formation of the essential axial structures (brain, spinal cord, eyes, ears, muscles, kidney tubes) of an embryo.

A developing organism is thus a system struggling with the help of its ancestral tendencies to survive and to convert itself into successive viable shapes. It is in the various requirements of these conversions and substitutions that the retention of many ancestral and apparently functionless structures finds its most satisfactory explanation, as Needham [32] has pointed out.

At the same time, the recognition of the subjection of developmental phenomena to natural selection raises other problems of great interest. One of these relates to the phenomenon known as 'double assurance', of which the formation of the lens of the eye in *Rana esculenta* may, as Spemann [35] says, be taken

as the best authenticated case. In this species of frog, the presumptive lens-forming area of the epidermis is already localized and fixed or determined, as regards its subsequent differentiation into a lens, at the early neurula stage. But the eye-cup developing beneath the epidermis at a later stage also possesses the power to induce the formation of a lens from the epidermis overlying it. This power is not normally exerted in *Rana esculenta*, but it is in *Rana fusca* where in the absence of the eye-cup the lens does not develop. In *Rana esculenta*, therefore, there are two mechanisms each of which can result in the formation of a lens. One of these mechanisms involves the determination *in situ* and from a distance of a region of epidermis in some as yet obscure manner, in relation to the organizer and the geometry of the whole embryo; the other involves the diffusion from the eye-cup of a chemical substance the effect of which is to induce the epidermis on which it acts to form a lens. The two mechanisms thus involve different kinds of processes, and their existence raises the problems as to how these mechanisms are directed to the same end-result, and how the 'additional' mechanism was evolved if one alone would give the organism survival value against the rigour with which natural selection would treat a lensless eye.

Perhaps, after all, the processes involved in 'double assurance' are not supplementary but complementary. Lehmann [29] has drawn attention to other cases of 'collaborative developmental unity', which lead him to find an analogy between the structure developed as a result of such collaboration and the principle of 'Gestalt' in psychology. Others will prefer to believe that such correlation or collaboration between mechanisms must find its explanation in some as yet undiscovered underlying event in the ontogeny—an organizer, or a gradient-field co-ordinate system—which has set the processes of both mechanisms at work.

An important concept in biology to which modern embryology has a contribution to make is that of homology. The usually accepted view of homology between structures bases the resemblance between them on the genetic affinity underlying them as structures descended, however modified, from a representative in a common ancestor. This concept is at the root of all phylogenetic schemes, for it is by means of their

homologous structures and the modifications which they have undergone that organisms are classified. The essential notion of homology as thus conceived is the continuity of structures in phylogeny and not the resemblance between homologous structures, for structures undoubtedly homologous may be very different anatomically and histologically (e.g. the pineal eye in reptiles and the pineal gland in mammals).

This concept of homology takes no account (and, as will be seen, rightly) of the distinction which may be made between genotypes and phenotypes. It holds that structures must have been present and visible all along the phylogenetic lines leading back to the point of divergence from the common ancestor if they are to be regarded as homologous. In other words, the concept is one of homology of phenotypes.

It is possible that, in requiring the visible presence of structures as far back as the point of divergence from the common ancestor, the theory of homology may in some instances be over-exacting. There seem to be cases (e.g. horns in titanotheres) in which the independent appearance of closely comparable characters in related but divergent stocks is more satisfactorily explained, as by Huxley [25], on the lines of genetic affinity; the manifestation of the character in the common ancestor having been obscured or delayed for developmental reasons, involving questions of growth and magnitude. Such cases are covered by the expression 'latent homology'.

It is, of course, obvious that, in so far as homology implies a common descent, it must involve genetic affinity. But the results of recent advances in genetics have shown that genes are not restricted in their sphere of influence to the characters which they have been found to control in a normal environment and a normal gene-complex. Further, under varied conditions of the gene-complex, a gene may cease to control the formation of one particular character, and, instead, may control another completely different character. Thus in poultry, as Fisher [9] showed, a gene controlling the formation of a crest of feathers also produces cerebral hernia. In the wild type, the gene behaves as a dominant in respect of crest, but as a recessive for hernia. The action of the gene on hernia can be entirely suppressed in certain gene-complexes (such as that of the Japanese silky fowl) while the production of crest is unaffected. There

is no homology between crest and hernia, and therefore it is clear that *characters controlled by identical genes are not necessarily homologous*.

There is another sense in which this statement is also true. Even where a character in two related organisms can be shown to be under the control of a single gene, and this gene can (by crossing) be proved to be identical in each, the characters may nevertheless not be homologous in the usually accepted sense. For it is possible that the common ancestor may not have possessed these characters, and their appearance may have been due (as in the case of 'white eye' in *Drosophila*) to independent and parallel mutation in the two stocks. Such cases would perhaps fall under the heading of 'latent homology' (see above), since the fact of mutation at the same locus may reflect an inherited common tendency.

On the other hand, the control of a character normally effected by one gene may come to be assumed by other quite different genes. A good example of this possibility is provided by the gene controlling the formation of the eyes in *Drosophila*, the recessive allelomorph of which produces the eyeless condition. Nevertheless, in homozygous eyeless stocks, the other members of the gene-complex can be reshuffled (by inbreeding) and recombined in such a way that they 'deputize' for the absent normal allelomorph to the 'eyeless' gene, and eyes reappear in the stock. Such eyes must be regarded as homologous with the eyes of the normal wild stock, and therefore it is clear that *homologous characters need not be controlled by identical genes*. Since this may be the case even when the homologous characters are identical, it is likely that when homologous characters do not resemble one another closely the genes controlling them may be very diverse.

Another sense in which this statement is also true concerns the action of 'mimic' genes—different genes with identical effects. Examples of these are provided by many cases of albinism in animals, and in plants Harland [19] has drawn attention to the existence of three different ways in which homologous characters may be produced genetically. He has summed up the position very aptly by stating that

'a character or organ is not genetically in a static but in a dynamic condition. The genes, as a manifestation of which the character

develops, must be continually changing, according to whether their allelomorphs are selected to strengthen other physiological processes. There must be continual competition between different organs or functions for one or the other member of a pair of allelomorphs. On the dynamic view of organs and functions we are able to see how organs such as the eye, which are common to all vertebrate animals, preserve their essential similarity in structure or function, though the genes responsible for the organ must have become wholly altered during the evolutionary process. . . .' (see also p. 94)

To which may be added that the evolution of the genetic control of a character must be regarded as having involved not only the substitution of allelomorphs for genes already concerned, but also the introduction of other genes to the control.

The genetic link between homologous structures cannot be analysed down to individual genes, but must be based on the gene-complex or such portions of it, or groups of genes, which control the structure in question. The individual members of these groups of genes may, during phylogeny, become changed by substitution, addition, or loss, so that, on the analogy of the two new blades and the new handle of the penknife, the groups may come to contain few or none of their original members. In other words, *the homology of phenotypes does not imply the similarity of genotypes.*

The analysis of the concept of homology in terms of single genes therefore breaks down. It is of great interest to find that an analysis of homology in terms of cellular or precellular correspondence of position in ontogenetic development likewise fails.

The study of homologous structures has hitherto tended to consider them as structures fully formed, or, when their development was considered, as structures arising simply out of the tissues which supply their substance. But the necessity of a consideration of morphogenesis in addition to morphology is becoming increasingly apparent. For instance, in gastrulation, as Pasteels [34] has shown, the forms of gastrulae can only be compared very unsatisfactorily, whereas the tissue-movements involved in gastrulation (extension of ectoderm, convergence and epiboly of chorda-mesoderm, invagination of endoderm) show some fundamental similarities, though differing in extent and in time-relations.

Another aspect of the importance of morphogenesis is shown by the fact that many structures owe their existence to a process of induction by special regions of the embryo known as organizers. To give a familiar example, the neural tubes have been regarded in themselves as homologous throughout the chordates, as no doubt they are. But in addition to the correspondence between those portions of ectoderm forming the neural tubes there is a more deep-seated correspondence between the organizers, the primitive gut-roofs which have been shown in fishes, amphibia, birds, and mammals to be active in inducing the formation of the neural tubes out of the ectoderm overlying them, and without which there would have been no neural tubes at all.

Clearly, the homology between the neural tubes in these classes of chordates is partly a result of the homology between the gut-roofs. An interesting attempt has been made by von Ubisch [39] to show at all events an analogy between the primitive gut-roof of chordates which possesses such remarkable organizing powers, and the hydrocoel of echinoid larvae, which is likewise a derivative of the wall of the archenteron, and induces the formation of the echinus rudiment, as MacBride [30] showed. At all events, there seems to be a common property of organizing power in the region of the blastopore, the opening of the archenteron in coelenterates, echinoids, and the chordates enumerated above. In addition, a large number of secondary organizers are now known.

It might seem, then, that in considering the homology of any given structures it is necessary to consider not only the tissues from which they arise but the organizers which have induced their formation. This does not mean, however, that the homology between structures is nothing but the homology between their organizers, and it would be a fatal mistake to deny any significance to the reacting tissue from the point of view of homology. A warning against this danger is provided by experiments in which the blastomeres of developing ascidians are disarranged. It appears from Tung's [38] results that the neural tube of the ascidian tadpole is not dependent for its formation on the activity of an underlying organizer; but this does not invalidate the homology of the ascidian tadpole's neural tube with that of other chordates in which it is so

dependent. However, in the ascidian tadpole it is interesting to note that the formation of the sense-organs in the neural tube is dependent on the underlying notochord. Other experiments which point in the same direction are those in which urodele belly epidermis is grafted over the mouth region of anuran embryos, and reciprocally. In each case the underlying host tissue organizes the graft and induces it to differentiate into mouth epidermis with lips. But on the anuran host the urodele epidermis produces enamel organs for proper teeth, and balancers (both of which anuran embryos lack); while on the urodele host the anuran epidermis produces horny teeth and suckers (both of which urodele embryos lack).

The grafted tissues have thus responded in a general way to the host organizers and given rise to buccal epidermis. But as the host organizers can hardly be regarded as capable of inducing structures which the sub-class of vertebrates to which they belong do not possess, these results must be taken to mean, not as Holtfreter [24] suggests that there is a distant homology between the horny teeth of anura and the true teeth of urodela, but that within each group both organizer and reacting tissue are active in controlling the type of structure produced. In this connexion, it is of interest to refer back (p. 64) to the case of the lens of the eye in the two species of *Rana*, for the lenses are clearly homologous, although in *R. esculenta* the lens is determined *in situ* via the gradient-field co-ordinates of the whole embryo, and in *R. fusca* the lens is induced by the optic cup. This case represents a stage in the substitution of one organizing mechanism for another, the overlap in time between the mechanisms being the explanation of the 'duplicity' of the 'assurance'. But the important point to notice is that *structures can owe their origin to different organizers without forfeiting their homology*.

The question next arises whether the reacting tissues which are induced to form a structure must also be 'the same' if the structures formed out of them are to be regarded as homologous. If by 'similarity' of tissues is meant similarity of position in the fertilized egg or early embryo, then clearly homologous organs can arise from material of dissimilar original location. Organ-forming substances for corresponding structures may be found in different places. Larval mesenchyme arises from

different quadrants of the cleaving egg in platyhelmia, nemertines, and annelids; the presumptive mesoderm lines the ventral lip of the blastopore in tunicates but the sides of the dorsal lip in craniates. Often, as in *Dentalium* and in tunicates, there is evidence of extensive translocation and rearrangement of organ-forming substances. It was pointed out by Jenkinson [26] that structures as obviously homologous throughout the chordates as the gut might be formed from the roof of the archenteron (Selachii, Teleostei), from the floor of the archenteron (Cyclostomata, *Ceratodus*, Urodela), from both roof and floor of the archenteron (*Lepidosiren*, Anura), from yolk-cells in the floor of the cleavage cavity (Gymnophiona), or from the lower layer of the blastoderm (Amniota). If these sources are plotted back into the egg, it will be seen that they occupy very different positions.

The ganglion of the trigeminal nerve contains neurons belonging to the general cutaneous functional component, and these arise typically from the cells of the neural crest. But in the frog, as Knouff [27] showed, these neurons arise from an epidermal placode and not from the neural crest. In the course of phylogeny there has thus been an alteration in the site of origin of these structures in ontogeny. It may further be remembered that homologous structures need not arise from the same segments of the body; in other words, the site of origin of a structure may vary along the antero-posterior axis of an organism, as Professor Goodrich [15] proved.

The fact is that *correspondence between homologous structures cannot be pressed back to similarity of position of the cells in the embryo or of the parts of the egg out of which the structures are ultimately composed.* It follows, therefore, that the best criterion for homology is comparative anatomy, and it is still possible to hold as did Étienne Geoffroy de St Hilaire [37] more than a century ago: 'the only general principle which can be applied is given by the position, the relations, and the dependencies of the parts, that is to say, by what I name and include under the term of *connexions.*' These are now more usually referred to as morphological relations, and it is their general constancy which gives them their value. Variation in morphological relations of homologous structures sometimes occurs, as, for instance, in the skull. But in these cases it is usually possible to find some

special reason for the departure from type. In any case it should be noted that, since the developmental mechanisms of homologous structures can become changed, the wonder is, not that morphological relations sometimes may vary, but that they are usually so remarkably constant. From these morphological correspondences, presumptions of community of descent may be obtained, and the probability of their correctness raised with the increasing number and refinement of the correspondences. But the interesting paradox remains that, while continuity of homologous structures implies affinity between organisms in phylogeny, it does not necessarily imply similarity of genetic factors or of ontogenetic processes in the production of homologous structures.

Out of the problems discussed above, referring to the site of origin in ontogeny of homologous structures, there arises the question of the germ-layer theory.

In the cases so far considered, the variation in position of the materials forming homologous structures has not gone beyond that generalization. The germ-layer theory, which is merely a deduction from the facts of ontogeny presented by organisms at different levels of the evolutionary scale, has so often been misunderstood and perverted that it may be of service to restate it briefly. It says that in the course of development *from the egg* the materials out of which the various primary structures arise are disposed simply in layers, and that homologous structures have been consistently found to arise from corresponding layers.

A plea may, perhaps, be entered here for more rigorous logic and nomenclature in modern embryological work concerning the germ-layers. Particularly in those forms in which cleavage results in the formation of a blastoderm, it is regrettably common to find the statement that the notochord or the mesoderm is 'formed from the epiblast or ectoderm'. The mistake is to regard the superficial layer of the blastoderm as equivalent to epiblast or ectoderm, merely because it is external. There would be as much justification for the claim that in amphibian development the endoderm is formed from the ectoderm, merely because the material which is going to become endoderm is on the surface of the blastula before gastrulation. The fact is that it is impossible to speak of the germ-layers until they are

completely segregated. The superficial layer of the blastoderm should be given a non-committal name such as 'upper layer': it does not become ectoderm until the notochord and mesoderm have been separated from it. Neglect of these principles renders futile any attempt to compare the modes of development of forms with and without blastoderm formation.

The fact that in asexual reproduction (as in Polyzoa or Tunicata), regeneration (as of pieces of nemertine worms anterior to the mouth), and in operatively mutilated or modified embryos, structures may arise from a layer which would not have given rise to them in development from the egg, does not in any way detract from the value of the germ-layer theory as a generalization covering the events of normal ontogenetic development. What asexual reproduction, regeneration, and operatively modified embryos do show, however, is that the segregation of the germ-layers is *not* accompanied by any determination or fixation of fates, except for the tissue of the organizer, which is determined very early.

It has been abundantly proved that organizers can act upon tissues other than those upon which they normally act, that they can induce presumptive epidermis to differentiate into myomeres or pronephric tubules, and so on, as Mangold [31] has shown; and since the germ-layers are known to be in a large measure still plastic, the question may be asked whether, in exceptional cases, structures may not be formed from tissues of the 'wrong' germ-layer.

Allegations of failure of the germ-layer theory to cover certain facts of development have not been wanting, but in no field of biology is greater prudence necessary in coming to a conclusion than here. An example will make this clear. In amphipod crustacea, spiders, and scorpions, the Malpighian tubes arise from the endodermal midgut and are connected with it. In an insect such as *Vanessa* the Malpighian tubes arise from what appears to be the proctodaeal ingrowth. Since the proctodaeum is typically an ectodermal invagination, this might be regarded as evidence for the ectodermal origin of Malpighian tubes in insects, and, as Baldwin Spencer [3] contended, for their non-homology with the Malpighian tubes of spiders, crustacea, &c. But here it has to be noted that in some insects the endoderm is delayed in its appearance, so

much so that when it is formed from the blastoderm, it is carried into position in two separate portions, at the tip of the stomodaeal and proctodaeal invaginations, as Eastham [8] has explained. And so the Malpighian tubes of insects may nevertheless be of endodermal origin, as Henson [20] has pointed out, in spite of presenting the appearance of origin from the ectodermal proctodaeum.

The fact is, as this example once more shows, that things are not always what they seem. For a long time the mesoderm in the frog was regarded as formed by delamination *from* the wall of the archenteron. But the *intra vitam* staining method devised and practised by Vogt [40] enabled him to show that the future mesoderm zone is already distinct from the endoderm zone in the blastula. It is owing to the mechanical exigencies of the process of gastrulation that these zones become apposed to one another on their passage through the blastopore; their subsequent separation or 'delamination' does not represent any community of origin.

It must also be recognized that there may be variations in the paths followed by different regions of a germ-layer on their way to their definitive positions. Thus, in amphibia, the mesoderm of the trunk region is invaginated through the blastopore in the typical manner. But when the blastopore closes, the future tail mesoderm remains on the surface of the gastrula, having as it were failed to get in. Instead, as Bijtel [4] showed, it becomes involved in the formation of the hindmost part of the embryonic 'neural' folds, of which only the anterior four-fifths are destined to give rise to the neural tube. When these folds close over, the tail mesoderm (representing the hindmost one-fifth) finds itself in position, beneath the surface. It is mesoderm that has never been invaginated, but nobody would think, merely for that reason, of claiming that the muscles of the tail in amphibia were formed from ectoderm. As a matter of fact, the formation of the neurula has been shown by Goerttler [13] to be the direct consequence and continuation of the processes which bring about gastrulation. There is therefore a sort of dynamic connexion between the gastrulation of the trunk mesoderm and the neurulation of the tail mesoderm.

Another example of the fragmentation of a germ-layer during the manœuvres of gastrulation is provided by *Amphioxus*. In

tunicates the mesoderm forms a compact zone round the ventral lip of the blastopore, and is invaginated as such. But in *Amphioxus*, the foremost portions of the mesoderm on each side are detached from the remainder of the mesodermal zone, and lie like enclaves in the territory of the endoderm, with which they become invaginated, and from which they subsequently become pouched off to form the anterior head-cavities. The wall of the archenteron must rid itself of these before it can claim to be called endoderm, for nobody could deny the homology between 'gastral mesoderm' formed in this manner and 'peristomial mesoderm' which arises without relation to the wall of the archenteron.

There is, however, one set of phenomena which are very difficult to reconcile with the germ-layer theory, and these relate to the view, now widely held, that the cartilages of the visceral arch skeleton in amphibia are derived from the cells of the neural crest (for the literature on this problem, the reader is referred to the work of Starck [36]). If this contention be well founded, there would seem to be two possible ways of explaining it. The future cartilage-forming cells might be regarded as detached regions of mesoderm which have adopted a novel method of entry into the interior of the embryo, like the anterior head-cavities of *Amphioxus*. But this view involves the difficulty that the neural crest cells also have other fates, since some of them become neurons and others sheath-cells, for neither of which any mesodermal origin can be claimed. Or, the future cartilage-forming cells are not mesodermal at all, but originally ectodermal cells which have migrated into a position where an organizer determines their differentiation into cartilage regardless of their origin.

A comparable case, in which a complete disregard is shown for the origin of the cells of which an organ is composed, is that of the thymus. In *Salmo*, Deanesley [5] has shown that, while it starts as a thickening of the endodermal wall of the gill pouches, the differentiation spreads into the neighbouring ectodermal regions. In mammals, the work of Fraser and Hill [11] has shown that in *Trichosurus* the thymus is composed of tissue to which both ectoderm and mesoderm have contributed cells. In the mole the thymus is wholly ectodermal, while in the rabbit and in man it is wholly endodermal.

Fragmentation of germ-layers can hardly be appealed to here, and it is difficult, in considering this case, to resist the conclusion that an organizing agency is at work, inducing the differentiation of a thymus out of whatever material is available.

In each case in which a failure of the germ-layer theory is alleged, the facts must of course be determined on their own merits. But it should be realized that, if any of these exceptions to the theory be substantiated, they would constitute natural experiments proving two facts already known: viz. that the tissues of the germ-layers at early stages are plastic, and that organizers have the power of inducing the differentiation of structures out of whatever tissues are available to them. And the homology of such structures with structures formed from the 'normal' layer in other organisms could hardly be doubted, for as Pasteels [34] has rightly said, organs are not homologous *because* they arise from the same germ-layer, although they usually do. And the reason why they do is that they usually arise from roughly corresponding regions of the egg. All that the germ-layer theory can claim to do, therefore, is to generalize this fact.

In conclusion, attention may be turned to a recent tendency in embryological work, which is of interest because it shows how the wheel has come round full circle since the early days of the theory of evolution. Then, it was common to neglect ontogenetic causes since phylogeny was supposed to be able to explain everything; now, some authors who find ontogenetic causes for the formation and presence of certain structures, are for that reason inclined to deny those structures any phylogenetic significance!

As an example may be taken certain recent studies on the development of the bones of the skull. It has been known ever since Roux's work that bone is formed in certain regions under particular conditions of mechanical disturbance, of stress and strain. The dura mater surrounding the brain of a developing mammal is eminently such a region. Therefore, it is argued, the various bones, frontals, parietals, &c., represent nothing but the effects of local ontogenetic conditions, and from this point of view Augier [1] has been led to consider that there is no need for the notion of genetic affinity or homology between these bones and those of the ancestral forms.

These views neglect the all-important principle, recognized by Ray Lankester [28], that every ontogeny is a response of the developing egg to certain internal and external factors. For every structure ever developed there must be ontogenetic causes, but this is no reason for denying the existence of a background of genetic factors which impart to the organism the property of reacting to stimuli in such a way as to produce those structures. It is interesting to note that His [23], the introducer of 'mechanistic' ideas into the study of development, was careful to point out that the hereditary aspect of the phenomena was in no way affected. The fact is, as Professor Goodrich [16] has said, that every character exhibited by every organism is *both* 'inherited' (i.e. genes controlling its development have been transmitted from the parents) *and* 'acquired' (i.e. produced by the interplay of factors, genetic, internal, and external, as a response, during ontogeny). The homology of the supra-occipital bone from lower vertebrates to man does not imply any direct derivation (were it even possible to conceive it) of the bone in each generation from that of the parents; on the contrary, every single individual all along the phylogenetic line has developed the bone because it has derived from the germ-plasm the genetic factors enabling it to do so, and because in every single ontogeny the normal interplay of external and internal factors has resulted in the development of the bone.

On no other view is it possible to understand the relations between ontogeny and heredity. There is, however, a further point, of importance because it concerns the whole manner of approach to many biological phenomena. The events of ontogeny may be said to bear on the problem of evolution in so far as phylogeny is the result of successive ontogenies. But even a complete knowledge of the causes determining the succession of form-changes in ontogeny would still fail to provide an explanation of why ontogenies themselves have been modified so as to give evolution. Similarly, a complete knowledge of the phylogenetic history of an organism does not explain the causal connexions between the events of its ontogeny. As Huxley has pointed out, a living organism must be studied from two distinct aspects. One of these is the causal-analytic aspect which is so fruitfully applicable to ontogeny. The other is the

historical descriptive aspect which is unravelling lines of phylogeny with ever-increasing precision. Each of these aspects may make suggestions concerning the possible significance of events seen under the other, but does not explain or translate them into simpler terms.

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THE NATURE OF INTERSPECIFIC DIFFERENCES

By J. B. S. Haldane

THE analysis of interspecific differences is a prerequisite for any complete theory of evolution. Thus Darwin held that 'varieties are incipient species'. That is to say interspecific differences are of the same sort as intervarietal, though larger. On the other hand, later workers such as Bateson and Goldschmidt, on the basis of genetical work performed since Darwin's time, have held that the differences between species are qualitatively, as well as quantitatively, different from those between varieties.

The taxonomist generally distinguishes species on a morphological basis. Of recent years cytology, or rather karyology, the study of the nucleus, has proved an important adjunct to a study with the naked eye or the lower powers of the microscope. Bacterial species are largely differentiated on chemical grounds, e.g. by their capacity for fermenting lactose or staining with Gram's stain. Their immunological and pathogenic properties are also important specific characters. Finally, viruses are differentiated by their pathogenic properties; but their structure as revealed by X-rays is a morphological criterion which is likely to be important in the future.

Some species are strikingly plastic, notably plants such as *Ranunculus aquatilis* or animals such as *Amblystoma tigrinum* whose forms vary greatly with their habitat, and in which one form can be converted into the other. On the whole, plants are more plastic than animals. Clearly the distinction between species must be sought in those characters which are unaffected by the environment, and particularly in the hereditary factors which are constant throughout a species.

It follows that a genetical analysis will give a deeper knowledge of the nature of interspecific differences than a morphological. It is, of course, very much more difficult, and has only been carried out in a few cases. However, the fact that most hereditary differences within a species have been shown to be

determined by genes located in the chromosomes gives a peculiar importance to the study of chromosomes. A morphological study of the dividing nucleus may in fact give information of a different character from that derived from any other morphological study. Thus if a plant species has twice as many chromosomes as a similar species, we can predict that, if they can be hybridized, most of their hybrids will be sterile; while if the number and morphology are the same, the hybrids are more likely to be fertile.

I shall make no attempt to define a species. If Darwin was right there is no sharp distinction between a species and a variety. But a provisional definition must be in terms of genetics as well as morphology and habitat. As Ray wrote, *Nulla certior occurrit quam distincta propagatio ex semine*. For example, when Erlanson obtained several alleged species of *Rosa* from the natural seed of one plant, the claim of these forms to specificity lapsed. It is to be noted, however, that a genetical criterion will not always work. Thus the common dandelion *Taraxacum officinale* is apogamous and rather polymorphic. But no one seriously proposes to divide it into hundreds of species merely because the different forms will not breed together.

While two forms which will breed with their like but not with one another are certainly to be regarded as different species, it does not follow that forms giving fertile hybrids are not to be regarded as different species if they have different morphology and habitat, particularly if they are not connected by a series of intermediates. The clearest cases are those where the hybrids are only slightly fertile, or where one sex only is fertile.

Viability and fertility of hybrids.

The physiological barrier between two species may be of several different kinds. It may occur before or after fertilization, and the hybrids, if any, may be sterile, or more or less completely fertile. In animals which copulate, there may be a psychological, mechanical, or temporal factor preventing copulation. If copulation occurs, or if the gametes are discharged into water, there may be a barrier, seemingly of a chemical nature, to fertilization, or finally a failure of the zygote to develop.

If the zygote develops into an adult this is often more vigorous than either parent species. But even so, it may be wholly or

partially sterile. This sterility may be confined to one sex. It may further be due to two quite distinct causes. The process of development of the gonads may be so incomplete or anomalous that meiosis does not even start, or is grossly abnormal. Or, on the other hand, meiosis may begin normally; but owing to the non-correspondence of the paternal and maternal chromosome sets the chromatin cannot be equally divided at the first meiotic anaphase. Hence either gametes are not formed, or if they are formed the large majority contain so unbalanced a set of chromosomes as to give no viable offspring even when the hybrid is back-crossed to one of the parent species. Further, in the higher plants, where (particularly in the pollen tube) the nucleus is physiologically active, as it is not in animal gametes, the abnormal gametes may perish before fertilization.

Any of these agencies may prevent the effective crossing of species. The question of their evolutionary origin then arises. The usual Darwinian view was that a parent species, separated in two different geographical or oecological habitats, gradually diverged into two species under the influence of different selective systems. Finally, the differences became so great as to cause sterility. It was, however, pointed out that the different domestic races of the same species, which Darwin regarded as a model for the origin of species, were generally fertile together, and if so always gave fertile hybrids.

Some geneticists, and particularly Bateson, regarded this as a fatal objection to Darwinism. However, it is now possible, within a species, to induce changes which give rise to a variety which does not cross at all readily with the parent variety, or which gives completely sterile hybrids on crossing with it. So far these changes have been of an abrupt character. Hence some geneticists have taken the view that the barriers to crossing arise spontaneously, and that the morphological and other characters which differentiate the species develop later. This may sometimes be the case, but we shall find reason to think that it is not always so, and that Darwin was very possibly right in some cases at least.

The genetics of taxonomic differences.

The morphological and other characters which serve to differentiate species are often less striking than those which

differentiate varieties. Darwin held that varieties were incipient species. If so, these interspecific differences should be determined in the same way as intervarietal, and in some cases at least they are so. Where species cannot be crossed this question is clearly unanswerable at present in almost all cases. The exception arises when the normal form of one species resembles a variant of the other. For example, many dipteran species have wing vein configurations similar to those of *Drosophila* mutants, and it is a reasonable hypothesis that they are due to gene differences of the same kind.

It will be seen, then, that the results of genetical research on varietal differences within a species are certainly not irrelevant to the species problem. In what follows I shall develop the results briefly summarized above, in greater detail.

Polyploidy.

One important group of barriers to crossing arises directly from differences in chromosome number and structure. It is at once clear that numerical differences must have arisen abruptly, since the number of chromosomes is necessarily integral. The simplest case is that of a polyploid series. Thus in the genus *Rumex* (section *Lapathum*) the following numbers are found in somatic mitoses, the gametic numbers being half those given.

R. alpinus and 4 other species	20
R. maritimus and 2 other species	40
R. crispus and 2 other species	60
R. japonicus and 1 other species	100
R. andraeanus	120
R. hydrolapathum and 1 other species	200
R. obtusifolius and *R. pulcher*	20 or 40
R. britannicus	40 or 160
R. domesticus	40, 60 or 80.

There can be little doubt that the primitive number was 20, and that up to 10 sets of 20 may be accumulated in one cell. Further, the evolutionary process is actually going on within some species at the moment. It is probable that the varieties of the same species with different numbers have different habitats or habits, as in the case, e.g. with the diploid and triploid varieties of *Nasturtium officinale*, in which Manton has shown that

the English summer form is diploid, the winter form triploid. Wild polyploid forms of this plant are not found south of the Alps and Pyrenees. And it is likely that the different types cross with difficulty.

Polyploidy of this type may arise in two distinct ways. Autopolyploids may arise within a species by simple doubling or trebling. This can be induced by heat, physical injury, or chemical treatment, and occurs spontaneously. An autotetraploid may cross with the diploid form with great difficulty. Thus the autotetraploid *Lycopersicum esculentum* is very hard to cross with the diploid form, and the hybrids, being mostly triploids, are very sterile. As tetraploids differ from diploids in morphology and physiology, being often more resistant to cold, some species have probably originated in this way (e.g. *Avena elatior*).

Alternatively a tetraploid may arise from hybridization. Such allotetraploids contain two sets of chromosomes from one species and two from another, each set pairing within itself save for occasional exceptions which are a cause of variation. The doubling may arise in the somatic tissues of a sterile hybrid, or in other ways. Apart from artificial hybrids such as *Primula kewensis* (from *P. floribunda* × *P. verticillata*) the best authenticated instance is that of *Galeopsis tetrahit*, which was reconstructed by Müntzing from *G. pubescens* and *G. speciosa*.

Even intergeneric hybrids may be very vigorous and fertile. Thus *Triticum vulgare* and other 42-chromosome wheats have two sets of 14 chromosomes derived from a diploid or tetraploid *Triticum* species, and one set of 14 derived from an *Aegilops* species, as shown by their pairing properties.

Thus polyploidy is one method by which a barrier to crossing may arise, either before or after the origin of other differences. It has been responsible for a good deal of speciation in the flowering plants. But in many groups it is rare. Only one polyploid species is known in the gymnosperms, and polyploidy is rare in Metazoa, presumably because it interferes with the sex-determining mechanism. The polyploid races of animal species (e.g. of *Solenobia* and *Trichoniscus*) are usually parthenogenetic. And the only polyploid species which can be inferred with strong probability from a comparison of chromosome numbers are found in the hermaphrodite Mollusca and Annelida. But there

are probably polyploid series in Lepidoptera (e.g. in *Lycia*) and here the only artificial animal allopolyploids (in *Pygaera* and *Saturnia*) have been made. It is tempting, but probably illegitimate, to suggest that, since the Placentalia and many reptiles have about twice the chromosome numbers of the Marsupialia and of most Amphibia (e.g. *Homo*, $n = 24$, *Oryctolagus*, $n = 22$, *Dasyurus*, $n = 13$, *Triton*, $n = 12$) they have arisen by doubling.

Aneuploidy

A diploid and tetraploid race of the same plant often differ very little. A plant with $2n+1$ or $2n+2$ chromosomes differs a good deal more from a plant with $2n$ than does the tetraploid ($4n$). Such plants, however, rarely breed true. Even if the new balance produces a satisfactory zygote, the gametes with an abnormal chromosome number may be handicapped. Aneuploid plants, like polyploids with odd numbers, such as triploids and pentaploids, may, however, reproduce themselves by one or other of the forms of apomixis. The best examples of evolution by aneuploidy occur among secondary polyploids. In most of the Rosaceae the basic chromosome number is 7. For example in *Rosa* somatic chromosome numbers range from 14 to 56, through various multiples of 7; but in the Pomoideae the somatic numbers are 34, 51, and 68, the basic number being 17.

Darlington and Moffett made it highly probable that if the fundamental chromosome set in the Rosaceae be represented by ABCDEFG, that of the Pomoideae is $\begin{array}{l}\mathrm{ABCDEFG}\\\mathrm{ABCDEFG}\\\mathrm{ABC}\end{array}$. This is shown among other things by the observation of secondary pairing between bivalents, the closest configuration being three groups of three bivalents, and four of two. It is clear that such a change, probably in a plant with a somatic number of 28 or 42, must have been abrupt, and probable that the meiotic and other mechanisms then gradually adapted themselves to it.

Structural chromosome changes without numerical change

These can be detected in three different ways, which, in favourable cases, e.g. *Drosophila*, give concordant results: (*a*) the meiosis of a hybrid may be abnormal; (*b*) the gene arrange-

ments may differ between species; (*c*) the arrangement of the chromomeres in giant chromosomes, particularly the salivary chromosomes of *Drosophila*, may differ.

Taking species A as standard, species B may differ from it in respect of:

(*a*) Inversions. The order of genes or visible bands in A is *abcdefgh*, in B *abfedcgh*. Several inversions may occur in one chromosome.

(*b*) Reciprocal terminal translocations. Two chromosomes of A are *abcdef* and *ghijkl*, those of B being *abcdkl* and *ghijef*.

(*c*) Intercalary translocations. Two chromosomes of A are *abcdef* and *ghijkl*, those of B being *abef* and *ghicdjkl*.

(*d*) Internal duplications. A chromosome of A is *abcdefgh*. The corresponding chromosome of B is *abcdcdefgh*, *abcddcefgh*, *abcdefcdgh*, or *abcdefdcgh*.

(*e*) External duplications. Two chromosomes of A are *abcdef* and *ghij*. The corresponding chromosomes of B are *abcdef* and *ghcdij*.

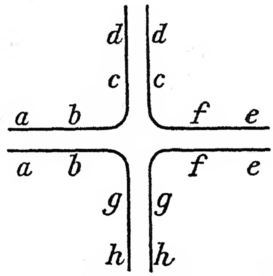
And combinations of these changes may occur. It is more doubtful whether non-duplicated parts of the chromosomes of A may be absent in B, except in the case of inactive chromatin, such as occurs in Y-chromosomes.

Inversions as differences between species were first discovered by comparing the gene maps of *Drosophila melanogaster* and *D. simulans*. These give sterile hybrids, but mutant genes in the two can be homologized. For example, in each of them two sex-linked recessive genes (or groups of allelomorphic genes) are known, which cause abnormal bristles. They are called 'singed' and 'forked'. Both in interspecific and intraspecific crosses 'singed' × 'singed' and 'forked' × 'forked' give abnormals, while 'singed' × 'forked' and reciprocally give normals. Thus the two loci can be identified. But they cannot be identified by inspection. Thus 'forked' in *simulans* is very like 'singed' in *melanogaster*. In the first and second chromosomes the order of the genes so far homologized is the same. Since the number homologized in the X-chromosome is 14, the homology is far-reaching. But there is a large inversion in one arm of the third chromosome.

A study of the cytology of Dipteran hybrid salivary glands

has greatly extended our knowledge. Thus *Drosophila pseudoobscura* and *D. miranda* differ in respect of at least 8 inversions in four different chromosomes.

Reciprocal terminal translocations are commoner in nature in plant than in animal populations, since where self-fertilization is possible they do not cause much sterility. They are readily detected, if the hybrid is sufficiently fertile to carry out meiosis. In this case a quadrivalent or higher polyvalent is formed and a certain proportion of abnormal gametes results. Thus the pairing of *abcd+efgh* with *abgh+efcd* leads to a quadrivalent which may be designated as



A more complex system of translocations gives a ring of six or more chromosomes. On these lines Blakeslee and his colleagues have analysed both geographical races of *Datura stramonium*, and also other *Datura* species. The different races of *D. stramonium* with 12 chromosome pairs give at most 2 rings of 4 when crossed with the standard type. Species crosses may give more complex patterns; e.g. *D. stramonium* × *D. discolor* gives 7 bivalents and a ring of 10 chromosomes. However, it is certain that the chromosomes of different species differ in other respects besides reciprocal translocations, since bivalents are often unequal. This does not seem to be the case with the geographical races of a species.

A fuller account of these and other interspecific differences is given by Darlington and Dobzhansky.

Combined structural and numerical changes

Each chromosome in a normal individual has one and only one centromere or spindle-fibre attachment, which pulls it to the poles during anaphase. If a chromosome has none it is

generally left on the plate; if it has two it is liable to be torn in half, one centromere going to each pole. Centromeres appear to be self-reproducing organs, so mere fragmentation of a chromosome will at best give a normal fragment with a centromere, and an acentric fragment. If therefore the number of chromosomes in a haploid set is to be increased by unity, one centromere, and probably the genes in its neighbourhood, will be duplicated, even if others are not. It is also probable, though not certain, that the ends of chromosomes are self-reproducing structures, not arising *de novo*.

Thus we should expect to find a chromosome *abcd,efgh* (where the comma represents the centromere) represented by *ad,efgh*+*abcd,eh* in another species. The hybrid should then form a trivalent during meiosis. Thus one chromosome of *Bombyx mandarina* pairs with two of *B. mori* in the hybrid. It is easy to imagine processes by which the number of chromosomes may be increased by one, each such step involving duplication of chromatin near the centromeres and perhaps near the ends. But the chromosome number can certainly be reduced in evolution. Thus some species of *Crepis*, a composite plant near the head of the evolutionary scale, have a haploid set of only 3, the smallest number in any plant; and small numbers are also common in the Diptera. If a reduction in chromosome number is not to involve a loss of vital genes with the lost centromere, it follows that the regions of the chromosome near the centromere must be inert, that is to say void of genes. This is the case in *Drosophila melanogaster*, and is likely to be generally true in groups where the chromosome number is low. It is also to be expected that the ends are inert, as they are at least in some chromosomes of *D. melanogaster*.

Genetical differences. Nucleus and cytoplasm

The question is often asked whether the differences between species are mainly determined by nucleus or cytoplasm. The statement is sometimes made that while nuclear differences may account for variation within a species, the deeper differences between species depend on the cytoplasm. In a few cases it can be simply and conclusively shown that all or almost all differences are determined by the nucleus. In five different phanerogam species crosses 'male parthenogenesis' has been recorded.

For example, Bleier found that the pollen of *Vicia sativa* on *Lens esculentum* gave plants indistinguishable from the paternal species, the maternal nucleus being extruded from the cell. In no case of 'male parthenogenesis' is any hybrid character recorded in the *adult* progeny.

However, enucleated fragments of echinoderm eggs which develop after fertilization by foreign sperm often show predominantly maternal characters in the larvae. The clue to the difference is found in the fact that genes often take a considerable time to influence the cytoplasm. Thus the direction of coiling in *Limnaea peregra* is determined by genes carried by the mother. So a dextral snail may be homozygous for sinistrality, giving nothing but sinistral progeny in all later generations. It is dextral because its mother had one gene for dextrality which determined the cytoplasmic architecture of all 'her' eggs. In *Bombyx mori* several larval colour characters are determined wholly by the mother's genotype. In *Ephestia kühniella* the eye colour of the adult is determined by genes in the normal way. But the colour of the larval ocelli follows that of the maternal eyes, gradually changing to the adult colour, whatever that may be, which is determined by the genes in the larva in question.

In the cross between *Triton taeniatus* and *T. cristatus*, Hamburger found that no paternal characters appeared before the limb-bud stage, though the adult hybrid was fairly intermediate. All this is in agreement with Harvey's remarkable observations on the development of enucleated echinoderm eggs. If two reciprocal hybrids are compared we may expect them to show maternal characters when young. If they are predominantly maternal when adult, this is not conclusive for cytoplasmic inheritance, as appears from the *Limnaea* case. Dobzhansky has made it very probable that the cytoplasmic differences between the races (or subspecies) A and B of *Drosophila pseudo-obscura*, which give sterile male hybrids, are determined in this manner. It is only when the difference is carried on into later generations that we can speak with any confidence of cytoplasmic differences not ultimately under nuclear control.

In species crosses within the genus *Epilobium* reciprocal crosses are sometimes different, though not very markedly so. By crossing the hybrids of *E. luteum* with pollen from *E. hirsutum* for 13 generations, plants were obtained by Michaelis and his col-

leagues with a practically pure *hirsutum* nucleus in *luteum* cytoplasm. These differed from *hirsutum* in several respects, e.g. broader leaves, greater branching, and higher resistance to certain moulds. There was, however, evidence that the plasma was being very slowly modified by the nucleus. Similar results have been obtained in other flowering plants and in mosses. In particular the chloroplasts may differ. But they are by no means usual. I know of no clearly demonstrated case of this sort in animals, though certain results in Amphibia strongly suggest it. The possibility that some of the plant results are due to infection by a benign virus, and indeed that there is no absolutely sharp distinction between virus infection and plasmatic inheritance, is worthy of consideration. It must be emphasized that these cytoplasmically determined differences are not peculiar to species crosses. They have been found within plant species, though rarely; but never so far within an animal species. They do not therefore constitute a sharp difference between inter-specific and intra-specific differentiation, though they are certainly commoner as a cause of the former. But it must be noted that both in plants and animals reciprocal hybrids are very often indistinguishable, so that the majority of differences between crossable species are determined by the nucleus.

The genetical analysis of interspecific differences

This very important problem has so far mainly been attacked in plants. A good example is furnished by Chittenden's analysis of the crosses between *Primula Juliae* and the primrose *P. acaulis* and oxlip *P. elatior*. The chromosome number in each is 22, and meiosis in the hybrids is regular and fertility high, though germination is poor both in *P. Juliae* and its derivatives. The following genetical analysis was reached by Chittenden. The species differ, *inter alia*, in respect of the following six genes, each being almost if not fully dominant.

A. Presence of anthocyanin in the petals.
D. Intensifies the anthocyanin if A is present.
I. Inhibits anthocyanin formation.
Y. Presence of yellow pigment (anthoxanthin) in the petals.
O. Presence of orange, as opposed to yellow, plastid pigment in the eye.
P. Pedunculate or umbellate inflorescence.

The constitution of a gamete of the three species is then:

Juliae	A D *i y p o*
acaulis	*a d i* Y *p o*
elatior	*a d* I Y P O

Most individuals of *elatior* were II, but two were I*i*. I does not completely inhibit anthocyanin under all conditions. The F_1 flowers of *Juliae* × *elatior* may show red streaks. The segregation in F_2 and in back-crosses corresponds fairly well to expectation, though numbers are not always very good, perhaps through selective germination, and one unexpected cream plant occurred in the cross (*elatior* × *Juliae*) × *elatior*. Chittenden gives a possible explanation for this. In F_2 white flowers (*aa yy*) occurred in the expected proportions of 1/16 (4 out of 68) from *acaulis* × *Juliae*, and 13/64 (18 out of 100) from *elatior* × *Juliae*.

Besides these genes Chittenden postulates three controlling the degree of hairiness. *Juliae* is semiglabrous, the other species very hairy, and the F_1 semiglabrous. The prostrate habit of *Juliae* is recessive in F_1, as is its reniform leaf shape. Here, however, segregation in later generations is complex. It is noteworthy, for a reason which will appear later, that structural characters not found in either parent, such as narrow petals and petals with frilled margin, appeared in F_2. The above analysis is typical of what is found in many plant species crosses where chromosome numbers are equal, and hybrids are fertile and have normal meiosis.

In animal crosses it is rare to find more than two or three characters displaying Mendelian inheritance due to a single gene, but characters which segregate sharply in F_2 or back-crosses are generally of this nature. The results obtained regarding colour in rodents are particularly interesting. *Cavia rufescens* is about half the size of the guinea-pig *C. porcellus*. It has banded hairs on its abdomen, whereas the wild *C. porcellus* has banded dorsal hairs and a yellow belly. The F_1 males are sterile, but the females are fertile, and by repeated back-crossing to the guinea-pig male fertility is finally re-established. The *rufescens* pattern is due to a gene A^t (ticked belly) which is allelomorphic with A^y (yellow belly of wild *porcellus*) and *a* (black of domestic varieties of *porcellus*). It is recessive to A^y and dominant to *a*. That is to say, the difference in colour between the

species is due to a mutation in the same gene as that which gave rise to the black variety, but not so large.

The same locus is responsible for the differences between *Mus musculus* and *M. bactrianus*, which perhaps hardly deserves specific rank, and between the geographical races of *alexandrinus* and *tectorum* of *Mus rattus*. These two races differ from *Mus rattus rattus* (the black rat) in respect of an allelomorph of *e* (recessive yellow). Once again we find relatively small gene changes responsible for differences between species or sub-species.

Harland arrived at the same conclusion as regards *Gossypium* species. For example, the mutant crinkled of *Gossypium barbadense* is recessive within the species. It is incompletely so in a cross with *G. hirsutum*. If the heterozygotes carrying the normal allelomorph of the crinkled gene *c* are repeatedly back-crossed on to crinkled *barbadense*, we finally obtain plants which are essentially *barbadense* except for a normal allelomorph of crinkled derived from *hirsutum*, and a few genes closely linked to it. It turns out that *G. hirsutum* in different races carries two allelomorphs of *c*, one giving intermediate heterozygotes, the other nearly but not quite dominant. Harland thinks that most genes in the two species may differ in this way, and that such slight differences account for the quantitative interspecific differences.

The majority of interspecific differences, however, blend, though there is usually an increased variability in F_2 which can be explained as due to segregation. Genetical analysis will only be possible by means of linkage, such as has been successfully applied in the tomato and other plants. The hypothesis of multiple factors is at present neither proved nor disproved. But the genetics of size in such a cross as *Mus musculus* $\times$ *M. bactrianus* is exactly parallel with that in a cross between large fowls and bantams. There is no reason to suppose that their genetical bases differ. In both the F_1 is intermediate, while the F_2 transgresses the parental limits.

Mendelian behaviour in crosses between diploid and allopolyploid species

When a diploid and an allotetraploid species are crossed the first cross are usually triploids which may form a complete set of bivalents. Thus we may represent the diploid as $\dfrac{\mathrm{A\,B\,C\,D\,-\,-\,-}}{\mathrm{A\,B\,C\,D\,-\,-\,-}}$,

the allotetraploid as $\begin{matrix} \mathrm{A'\ B'\ C'\ D'} - - - \\ \mathrm{A'\ B'\ C'\ D'} - - - \\ a\ b\ c\ d - - - \\ a\ b\ c\ d - - - \end{matrix}$, where letters stand for whole chromosomes. The hybrid is $\begin{matrix} \mathrm{A\ B\ C\ D} - - - \\ \mathrm{A'B'C'D'} - - - \\ a\ b\ c\ d - - - \end{matrix}$. The sets A B C D - - - and A′B′C′D′- - - are supposed to be so like that they pair regularly at meiosis, so that the gametes contain a regular set of chromosomes derived from them, and an irregular number of members of the set *a b c d* - - -. By back-crossing the hybrid to either parent species we can thus introduce parts of the A B C D - - - set into the tetraploid, or of the A′ B′ C′ D′ - - - set into the diploid. When the normal chromosome number is re-established we may expect Mendelian behaviour. Watkins found that such characters as keeled *vs.* rough glumes, waxy *vs.* waxless foliage, and others which distinguish *Triticum vulgare* ($2n = 42$) and *T. turgidum* ($2n = 28$), can be transferred in this way from one species to another, and are due to single genes. But Lammerts showed that as a result of crossing *Nicotiana rustica* ($2n = 24$) and *N. paniculata* ($2n = 12$), and back-crossing the hybrid to the parent species new types arise. The species only differ quantitatively. But when *paniculata* chromosome segments are transferred to *rustica*, and the normal chromosome number re-established, a number of dominant characters are obtained. At least six of them were due to single genes or to blocks of chromosome behaving as single genes. On introducing *rustica* chromosomes into *paniculata* twelve recessive types were obtained.

Some of the new types are described as more vigorous than normal. It would therefore seem that the chromosomes of *paniculata* type in *rustica* have evolved in their new situation, largely by recessive mutations; but that this evolution has not been merely degenerative. It may have evolutionary value, and if so it is a novel type of clandestine evolution.

Non-genetical evidence for single gene interspecific differences

Sturtevant pointed out that a number of the mutants of *Drosophila melanogaster* have characteristics (e.g. wing venation, eye colour) resembling other dipteran species. Beadle and

Ephrussi transplanted larval eye rudiments between larvae of this species, and showed that, e.g., a vermilion eye rudiment develops into a vermilion eye in a vermilion-eyed host, whilst in a cinnabar-eyed host it becomes normal. Thus vermilion and cinnabar eyes, which look much alike, may be distinguished.

Gottschewski and Tan transplanted rudiments between *D. melanogaster* and *D. pseudo-obscura*, which cannot be crossed, and identified mutant genes in the two. But they also concluded that the wild type of *D. pseudo-obscura* corresponds with the mutant 'clot' in *D. melanogaster*, and that in fact the two species differ in respect of this gene. Analogous conclusions could be drawn regarding genes concerned in anthocyanin production in higher plants.

Genic and morphological homology

The view was put forward by the author some twelve years ago that in related organisms homologous structures are developed through the action of homologous genes, and that therefore genic homology is more fundamental than morphological homology. This may often be true, but it has been shown by Harland not to be universally so. He found that all or almost all characters which exhibited simple Mendelian behaviour within the species *Gossypium barbadense* and *G. hirsutum* showed a certain degree of blending in the interspecific F_2.

In extreme cases, e.g. the F_2 between 'crinkled' *barbadense* and normal *hirsutum*, it was found that plants of genotype *cc* (where *c* is the gene responsible for crinkledness in *barbadense*) varied from a slight to a very exaggerated crinkled. Similarly the cross of *barbadense* crinkled and *hirsutum* crinkled gave a continuous range from extreme crinkled to apparently normal in F_2.

It is thus clear that within each species there is a series of modifying genes which, in their homozygous condition, ensure that a CC plant should be normal, and a *cc* crinkled, but not grossly so. But these modifiers differ in the two species, so that in the F_2, *cc* plants of very varying phenotype are produced. Thus the normal leaf in the two species depends not only on different allelomorphs of C but also on modifiers in different loci.

Similarly, when the above two species are crossed 1/16 of the F_2 are usually chlorophyll deficient, showing that chlorophyll

is determined by a different gene in each species. Here the two genes are probably found in the two different chromosome sets of an allotetraploid. But similar results were obtained for petal spotting in crosses of the diploid *G. arboreum* and *G. anomalum.*

It is now clear why abnormal forms often appear in F_2 of species crosses, e.g. *Rhinanthus*-like flowers in *Antirrhinum*. Homologous structures or functions may be determined by different genes in related species, and will be lacking in F_2 individuals (1/16 or less of the whole) where neither gene is present. This is analogous to the production of homologous adult structures by very different processes of embryonic or larval development (see p. 69).

Summary

A fuller discussion of these and other data will be found in the work of Dobzhansky [2], Darlington [1], and Harland [3], to which the reader is referred. Our general conclusion is that there is no evidence that at any rate closely related species differ in a manner qualitatively diverse from varieties. In fact Darwin was correct in regarding varieties as incipient species.

But while varieties often differ in respect of one or a few genes, species may differ in respect of hundreds. Cytoplasmic differences between species are commoner than between varieties. So are microscopically detectable cytological differences. And it is not of course impossible that interspecific differences may yet be discovered of a type which is not found within a species. For the present, however, economy of hypothesis forbids us to postulate such differences.

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THE FORMATION OF SPECIES

METHODS OF STUDYING THE EARLY STAGES OF EVOLUTIONARY DIVERGENCE IN ANIMALS

By O. W. RICHARDS

THE problem of the formation of species may be approached in two ways. Either the groups of individuals which taxonomists call species, races, or varieties may be studied comparatively in an endeavour to deduce how one group might have been derived from another. Or one may study the variation of one or two species intensively in order to arrive by induction at the supposed course of evolution. The first method may be termed that of *population analysis*, and its technique differs in degree rather than in kind from that usually employed by taxonomists, entailing greater refinement (e.g. the use of elementary biometrical methods) and some elementary genetics (i.e. at least determining which phenotypes are not fluctuations). The second method is that of *evolutionary genetics*; the main contributions from this direction have just been ably summarized by Dobzhansky [2] and will not be considered further in the present essay. Clearly both extensive and intensive methods are necessary if a general theory of species-formation is to be well founded.

Population analysis in its broadest sense might be made to embrace all taxonomy, but the term is usually employed in a more special sense to describe the analysis of large populations of a single species or set of closely allied species. The type of information supplied by such analyses will be found in such summaries as the work by Robson and Richards [8] or that of Dobzhansky [2]. It is proposed in the ensuing paragraphs to consider rather a field lying between population analysis in the strict sense and ordinary taxonomy, and particularly to examine how far the ordinary procedure of taxonomy can be adapted so as to provide data more relevant to evolutionary studies than it does at present. For convenience of reference this field of amplified taxonomy will be termed *taxonomic analysis*.

The attempt to use ordinary taxonomic data as the basis of theories about species-formation suffers from three main drawbacks. Firstly, the taxonomic description of species is usually insufficiently quantitative. Colour and shape are often difficult to express quantitatively in any case, but even where linear measurements are given they are not usually recorded in a form suitable for analysis. Standard deviations are rarely calculated even where averages are recorded, and it is therefore impossible to know what weight can be given to such statements as 'two species differ in average size'. Secondly, as is all too well known, the taxonomic categories are of very different value in any extended series of animals. It is impossible, with existing methods, to state whether two species, say, of mammals differ from one another as much and in the same way as two species of birds. The attempt to make such terms as *species* or *variety* more precise has hitherto been unsuccessful. Thirdly, it is only in a few favourable examples that we know anything of the heredity of the characters which the taxonomist describes and we are liable to generalize from a number of examples which are not really comparable, e.g. treating all melanic varieties as of the same nature without genetic investigations. Unless these difficulties can be partly or wholly overcome, taxonomic analysis can only make a very small contribution to evolutionary theory compared with genetics. It is profitable therefore to consider how far recent studies have improved the position; whether they have shown that the method is valuable even if they have not provided enough evidence to found theories.

It should be stated in the first place that in many groups the preliminary arrangement of animals into genera and species is not yet sufficiently advanced for any refinements to be practicable at the present time. In such groups as the Acarina or the parasitic Hymenoptera, no working taxonomist can have the leisure necessary to undertake more than what may be termed routine taxonomy. All taxonomists nevertheless are aware that the standard of description has been subject to continuous improvement. In the present connexion it may be noted that the number of specimens examined is now usually stated, and that in many groups linear measurements of a number of parts of the body are recorded as a routine.

In special studies such as those of Crampton [1] on *Partula*, Sumner [9] on *Peromyscus*, &c., the standard deviations of the measurements are given as a matter of course, and in several fields of ordinary taxonomic practice it would be a very slight innovation to calculate this parameter as a routine. It is the purpose of the present essay to stress what could be done by ordinary taxonomists with slight changes in their methods rather than to put forward an ambitious programme of which the fulfilment would entail giving up all ordinary taxonomic work.

Before considering taxonomic analysis in greater detail it is necessary to define rather more clearly the relation between it and ordinary taxonomy.

If one had a number of specimens which might perhaps be made up of two species mixed together, the normal practice of a taxonomist who was studying them would be as follows. The specimens would be divided into two groups on the basis of any character which showed considerable variation in the series. A search would then be made for other characters correlated with the primary one. If none could be found, a division into two would be made on the basis of another variable character and a second search would be made for correlations. If two sets of correlated characters could be established the taxonomist would divide the series into two groups, though whether he would regard the groups as species or not would depend on a variety of other considerations. This process may be called semi-objective, since actual correlation-coefficients are not calculated and the amount of intergrading between the two groups is realized intuitively rather than expressed in figures.

I believe that the main framework of taxonomy will always have this intuitive background. The ability to pick out those master character-differences with which others are correlated is what is called 'having an eye for a species'; it is a faculty which is to a large extent innate though naturally it can be much improved by wide experience in the study of particular families or orders. The division of living organisms into groups defined by correlated characters must come first, and the quantitative taxonomic analysis afterwards. As a general rule the application of purely quantitative methods to a mixed set

of animals which had not been subjected to a preliminary sorting would be a waste of time and would not lead so quickly, if at all, to the recognition of whatever distinct groups were present. But there is a tendency not only to rely too much on the intuitive method but to ignore or to underestimate characters on which it cannot conveniently be exercised.

Thus two species will usually be separated by a rather small number of characters in which they differ qualitatively (at least superficially) or grossly quantitatively. But in many pairs of species almost every part of the body is found to differ in the average of some attribute if appropriate measurements are made. In ordinary taxonomic procedure those characters are stressed which are most discontinuous and most easily appreciated by eye. Linear measurements which only differ on the average are of much less practical use for identification, but in so far as they are correlated with 'taxonomic' characters they are equally fundamental indicators of specific divergence. In my experience the vast majority of the structures of two species which it is possible to measure[1] are found to differ significantly in the means of the measurements. The same deduction was made by Heincke [4] in his study of the herring and by Zarapkin [10] in his examination of certain beetles of the genus *Carabus*. A general preliminary conclusion, therefore, is that measurements of characters often of a type not supposed by taxonomists to exhibit specific differences may nevertheless reveal them, and that it is probably to a large extent justifiable to regard deductions from such quantitative measurements as applicable to specific differences in general.

I believe that this conclusion may have to be modified somewhat in very variable species or where the characters are very susceptible to environmental influence. Thus Zimmermann [11], after his studies of colour variation in *Polistes* (Vespidae), came to the conclusion that colour differences were due only to local climate and that no genetic geographical differences were involved. From my own studies of *Vespa*, however, I suspect that this may be only partially true. The colour pattern in general is so susceptible to climatic influence that fundamental geographical variation may be masked, and it is

[1] Or of which the variation can be divided into arbitrary classes whose frequencies can be determined.

therefore necessary to employ the usual intuitive procedure to determine which elements in the pattern should be measured if geographical diversity (more or less independent of climate) is to be established.

Finally, it may be suggested that if on measuring a number of characters in two groups (reputed species) it was found that the means did not differ significantly there would be strong grounds for believing that the groups differed rather in one or two genes (not affecting the characters measured) than in the large number which probably separate most species and races. In fact the commonness of quantitative differences between 'good' species may well be regarded as another aspect of the manifold effects of single genes. When two groups differ in many genes, all parts of the body are likely to differ in average measurements.

It is true that many features of pattern and colour are difficult to express in a quantitative way. Even a continuous range of colour, however, can be classified and the frequency of the classes enumerated as in Fisher and Ford's study [3] of the colour variation of noctuid moths. The difficulty of quantitative measurement of colour, pattern, sculpture, hairiness, &c., is more one of having time to do the measurement than of the impossibility of devising ways of measuring. A taxonomist rarely has the time necessary to deal fully with characters not susceptible to linear measurement, but even the separation of continuous variation into several arbitrary classes of which the frequencies can be given would be of great advantage. Evidently some characters would always be difficult to deal with and nearly all would require special studies to be measured at all completely. Nevertheless, large advances in the theory of species-formation would be possible if even only those characters capable of linear measurement had been fully recorded in a wide range of species. Moreover, when genetical methods are employed, only a few of the characters in which species differ can be analysed; no method can deal with all the characters of a wide range of animals. It may be suggested that for many purposes taxonomic analysis could be confined to characters capable of easy quantitative expression, just as evolutionary genetics deals only with a particular selection of variants.

If it is accepted that for many purposes it is sufficient to deal only with characters which can be quantitatively expressed, it is possible to put forward suggestions for improving the definition of taxonomic categories. Such attempts at improvement have been so uniformly unsuccessful in the past that it is necessary to avoid exaggerated claims. No magic criterion for recognizing good species can be brought forward, nor indeed have all the methods discussed in the next paragraphs been tried out enough to know whether they would be widely useful. In essence, all the methods actually proposed are tests of homogeneity. If these tests had been made on a sufficiently wide range of animals, it would be possible to state in accurate terms what amount of variation is to be expected in groups of various rank in the taxonomic hierarchy or in groups inhabiting geographical or ecological territories of different sizes or varying diversity. This would have a special value in dealing with sub-specific groups such as the so-called 'biological races', where ordinary taxonomic methods often break down. There would further be opportunities to study more accurately the relation between variation in structure and variation in the external environment. Finally, it might well be possible to make some generalizations about species, as a whole; it is clear that one could usually discuss normal specific variation within a single family, but it is probable that, at least in some respects, certain common attributes might be found for all animal species.

It has already been possible in groups such as the birds and mammals, where the making of a number of linear measurements has long been routine taxonomic practice, to make several important generalizations. Such are the 'laws' of Allen, Gloger, and Bergmann recently discussed in detail by Rensch [5, 6]. It was, it might be said, an accident of taxonomic practice that enabled Rensch to extend these laws so widely, i.e. an accident that in certain groups appropriate measurements were recorded in the ordinary literature of taxonomy. In most invertebrates it would be impossible to test the validity of the laws even if one wished to do so since measurements of that type are not usually recorded.

It is also, in all probability, largely a matter of chance whether the measurements made by taxonomists are such as to

enable generalizations like Allen's law to be founded on them. It is possible, for instance, that no general relation between climate and the relative length of the legs in the Arthropoda (such as exists in some mammals) could be discovered. Nevertheless, as previously suggested, almost any extended series of measurements would provide valuable material for studying the normal range of variation in species and other groups and for establishing the type and amount of correlation between separate characters.

If it be admitted, then, that the averages of a series of linear measurements (or other quantitative characters) are likely to be just as good specific characters as features regularly used by taxonomists, the method of taking such measurements may be examined and the use to which they might be put considered in more detail. Evidently only very general statements can be made about the sort of measurements which should be recorded; this will largely be decided by what is convenient or possible in each group of animals. On vertebrates, because of their larger size, it is easy to make a variety of linear measurements, and this is already the practice of taxonomists. To make their data more useful all that is required (where all figures are not published) is to record beside the mean and extremes and number of specimens examined, the standard deviation of the sample. In Arthropoda, linear measurements (except one or two which are necessary to indicate absolute size) are usually more troublesome to make. In any forms, however, with appendages made up of a variable number of segments, the enumeration of these is relatively easy. In other cases the number of spines or bristles on some organ can be counted. There are few animals having a hard skeleton which do not provide some character of this type. The characters could, at least in theory, as well be drawn from the early stages of the animal or from such features as egg-number or respiration-rate. It would probably be safer, however, to investigate the early stages separately in all species where they lived under very different conditions from the adult.

The second important point is how many different measurements must be made if anything beyond certainty of identification is aimed at. This question again can only be answered in very general terms. It is surprising how few different measure-

ments may lead to absolute certainty in the separation of two distinct though variable species. Frequently, if three separate characters have been treated quantitatively, almost every individual can be relegated to the correct group on these measurements alone, even though the characters dealt with are not those regularly used by taxonomists for separating the species pair in question. As the two groups approach one another more and more closely more and more measurements are necessary to obtain equal certainty. Heincke [4] used this method to identify the race or shoal to which individual herrings belonged. For this purpose it was necessary to measure twenty-four characters (with forty-one others in some cases) and to analyse the figures a little more deeply.

Heincke's main generalization was that the deviations of the separate characters of an individual from the means of the racial measurements (of the same characters) are normally distributed, just as are the measurements of a single character in a number of individuals of a species. In the actual case of the herring the mean measurements of many characters of the several races are known, and the deviations of the measurements of any individual from these means can at once be obtained. It is then possible to make use of the well-known fact that the mean of a series of members is a quantity such that the sum of the squares of the deviations of these numbers from it is a minimum. Thus, if an individual herring is compared with the several races to which it might belong, it can be assigned to that one whose means give a minimum for the sum of the squares of the deviations. In actual practice the assignment of an individual to its race is often possible by mere inspection if a considerable number of characters has been measured.

Zarapkin [10], however, points out that the herring is an unusually suitable animal for such studies since it lives in a relatively stable environment. In many other animals, especially invertebrates, the absolute size of the individual is easily affected by external factors, and this in turn has a marked influence on the magnitude of the deviations from the racial mean. This difficulty can, as he suggests, be largely overcome by dividing each deviation (in the particular individual studied) by the standard deviation of the measurements of the corresponding racial character. Zarapkin's actual method when

comparing two races is as follows. The means and standard deviations of a number of characters are determined for each race. If then it is desired to see if a particular individual belongs to a race, the deviation of each character from the mean of the race is divided by the standard deviation of that racial character. The quantities so obtained will fall on a normal curve of error if the individual belongs to the race, but will be irregularly arranged if it does not. The irregularity is usually so great (even as between two geographical races) that it is obvious on inspection. Unfortunately, in this particular form, the method is only applicable to very special cases, especially those where the correct assignment of individuals is of the greatest importance; for to decide whether the deviations fall on a normal curve or not requires that a very large number of separate characters be measured (Zarapkin actually measured 117). There are, of course, standard methods for determining the likelihood that a deviation of any particular magnitude should be found in a given, presumed homogeneous, population. While there is no doubt that methods of this sort are already of great value in determining in special cases how far a particular set of organisms is homogeneous, it may be suggested that if further data of this type were accumulated, they could be the basis of a routine taxonomic method.

Thus, if a number (say five) of characters had been measured in most of the species of a given family, it would at once be possible to say how much variability was to be expected in species of this group. Any species which showed a variability much greater than the normal would at once be suspected of some peculiarity in its make-up. It might in this way be possible to distinguish parasites with many hosts from those with one or with only a few; to distinguish multivoltine from univoltine species; or to recognize that some species were broken up into unsuspected local races. The proper application of this method would depend on having an estimate of the normal variability of a considerable number of species of a genus or family. It is doubtful whether such data exist at the present day, but two examples are given below of a preliminary trial of the method. An estimate of relative variability is found in the coefficient of variability (C = standard deviation divided by the mean and multiplied by a hundred). This quantity is not so much

affected by the absolute size of the animal as the standard deviation would be, but it is probable that a fuller statistical study of the problem might provide a better estimate of variability.[1]

EXAMPLE 1. Comparison of the variability of four characters in two solitary bees, *Andrena jacobi* Perk. (single brooded) and *Andrena bicolor* (Fab.) (double brooded). 74 ♀♀ of the former were measured and 91 ♀♀ of the latter (including some specimens of which the brood was not known). Figures for the separate broods of *A. bicolor* are also given. In each case the mean, extremes, and coefficient of variability of the character are given. The last three characters are measured in micrometer units, 355 units = 1 mm. In this particular comparison the single-brooded species is more variable than the double-brooded one. The discrepancy would be less if the standard deviation had been divided by the square of the mean (instead

Species		*A. jacobi*	*A. bicolor*		
Character	*Brood*	*One brood*	*Spring*	*Summer*	*Both broods together*
No. of hooks on hind wings	Mean	13·00	9·93	10·67	10·29
	Extremes	11–17	8–12	8–13	8–13
	C.	14·5	9·5	10·5	10·29
Distance between posterior ocelli	Mean	174·5	151·8	152·5	154·5
	Extremes	147–200	126–73	129–76	126–79
	C.	20·2	7·7	7·9	7·9
Wing vein I*	Mean	644·9	488·3	472·2	482·2
	Extremes	575–707	434–533	379–546	379–573
	C.	5·3	5·1	9·2	7·4
Wing vein II†	Mean	313·5	227·2	221·9	225·6
	Extremes	264–385	182–268	177–280	177–280
	C.	8·8	8·4	9·5	8·9

* Distance along vein $cu_1 + IA$ of forewing between *mcu* and first sector of $M3+4$ (Bradley's notation).

† Combined lengths of 2nd and 3rd sectors of *Rs* in forewings.

of by the mean). Although *A. jacobi* is rather closely allied to *A. bicolor*, there is of course no general information as to the

[1] It seems possible that it would be more satisfactory to divide the standard deviation by the square of the mean rather than by the mean itself. Another quantity, which might be called the 'mean deviation', appears to be worth consideration. This is obtained by finding the average of the deviations from the mean, deviations in either direction being counted as positive for this purpose. The average so obtained would be divided by the standard deviation.

amount of variability to be expected in the genus and the comparison of two species only is not sufficient. I am much indebted to Dr. W. N. Scott for making the measurements of these bees.

Example 2. Comparison of variability in the solitary bees *Colletes succincta* (L.) and *C. fodiens* (Geoffr.) with that in the bees parasitic on them, *Epeolus cruciger* (Pz.) and *E. variegatus* (L.). As each parasite has three or four species of *Colletes* as host, the parasites might be expected to be more variable. For comparison, a selected set of *E. cruciger* all of which were associated with a single host (*C. succincta*) is also given. The measurements are body-length in millimetres, for females only.

Species	*No. measured*	*Mean*	*Extremes*	*C*
C. succincta	79	9·96	8·5–11·5	6·90
C. fodiens	62	9·35	8–11	6·97
E. cruciger	312	7·63	5·5–9·5	11·76
E. cruciger attached to *C. succincta* only	56	7·91	6–9·5	9·54
E. variegatus	273	7·40	5·5–10	10·08

A second method of testing the homogeneity of a sample population involves the study of the correlations between characters. It appears to have some value in deciding which of various ways of grouping a set of organisms is most natural.

In the course of the systematic study of any animal group one commonly meets with two types of correlation. In the first type, two characters are either both present or both absent, but there is no correlation in the extent to which they are developed when both are present. In the second type, the characters exhibit normal correlation, that is the degree of development of one character is related (directly or inversely) to the degree of development of the other, at all stages. The first type of correlation ('presence or absence' type) probably arises whenever a species or variety becomes homozygous for two independent genes or sets of additive genes, which are not simultaneously controlled by absolute size or by external or other factors; the second type ('normal' correlation) when two genes or sets of genes are controlled by a common factor (e.g. absolute size, temperature, &c.). The sort of specific characters which taxonomists most delight in are correlated in the first

way, whereas metrical characters are usually, though by no means always, correlated in the second, at any rate within a *homogeneous* species.

The fact that the amount of correlation between some of the characters of a group depends in part on the homogeneity of the group indicates a method of testing whether a given group is homogeneous or not. It is, perhaps, a method of only secondary importance, but it has as yet been very little tried out. Sumner [9] in his account of the races of *Peromyscus* has discussed some aspects of this question, noting that correlations which hold within single races often break down in the species made up of a complex of such races. He suggests that this is intelligible on the assumption that the differences between races are almost wholly genetic (correlation, if present, of the 'presence or absence' type), whereas the differences between individuals of one race are mainly non-genetic (correlation of the 'normal' type). A study of correlation may, therefore, give an indication as to which racial or specific differences are mainly genetically determined, though here again the method is not one which would be used in a species to which the usual breeding tests could be applied.

If correlation coefficients are calculated it is necessary to have a theory by which to interpret them. A non-homogeneous group compared with a homogeneous segregate taken from it may show either a higher correlation coefficient between two characters or a lower one. The first case (increased correlation in the larger group) is probably less common but may be expected to occur occasionally if the characters happen to have certain numerical relationships in the two forms which have been mixed and if the two forms have been mixed in the right proportions.

The second case (increased correlation in a segregated group) is what would normally happen if the correlation between the two characters was mainly due to external causes. The increased correlation signifies, in this instance, that the differences between individuals of the segregrated group are mainly due to environmental causes (i.e. the group is now approximately of one genetic type). In general it may be suggested that if the segregation of a sub-group from a larger group significantly alters the correlation between two characters, there is a *prima*

facie case for considering that the larger group was not homogeneous. The following examples will illustrate this argument.

(1) Correlation decreased on segregation. In the females of the two British solitary wasps, *Ammophila sabulosa* (L.) and *A. campestris* (Pz.), there is no correlation between body-length and the fraction of the third abdominal tergite which is black (the basal part of the tergite is red). If the two species are mixed, however, a significant correlation may result. The example is a rather artificial one as the two species are, in fact, distinguishable in many characters.

Length in mm.		*14*	*15*	*16*	*17*	*18*	*19*	*20*	*21*	*22*	*23*	*24*	*25*	*Mean*
Frequency	*sabulosa* (36)	0	0	1	1	3	7	11	4	2	1	5	1	20·4
	campestris (10)	3	1	3	2	1	0	0	0	0	0	0	0	15·7
Fraction of 3rd tergite black (mean of specimens of each body-length)	*sabulosa*	..	..	·80	1·00	·67	·69	·70	·64	·60	·75	·72	·76	·70
	campestris	·35	·25	·28	·37	·50	..	..	..	..	..	..	..	·34

It is evident that there is no correlation between size and colour of the third tergite in either species but if the two be added together it appears that smaller specimens tend to have less black on the third tergite, though the relation is still irregular. Nevertheless, the correlation coefficient is quite high, $r = +0{\cdot}6032$, and is significant ($P < 0{\cdot}01$). In this case, therefore, segregation would result in reducing the correlation coefficient.

(2) Correlation increased on segregation. In a recent paper [7] I discussed the British races of the parasitic bees, *Epeolus*. There are two species, *E. variegatus* (L.) and *E. cruciger* (Pz.). One of the races of the latter is parasitic on the bee, *Colletes succincta* (L.). In all the *Epeolus* the number of hooks on the hind wings is correlated with body-length and this correlation tends to become higher as the group studied becomes more homogeneous. Thus:

Correlation of number of hooks on hind wings with body-length.

E. cruciger (311♀♀) and *E. variegatus* (259♀♀) added together $r = +0{\cdot}2538$ ($P < 0{\cdot}01$)
E. cruciger (311♀♀) alone . . . . . . $r = +0{\cdot}4065$ „
E. cruciger (56♀♀) race attached to *C. succincta* . . $r = +0{\cdot}5943$ „

All these correlations are significant, as is the difference between

the first two. The second pair of coefficients do not differ significantly. It may be said, therefore, that the removal of the specimens of *E. variegatus* leaves a more homogeneous group; on the evidence brought forward here it cannot be said that the group of *C. succincta* parasites is more homogeneous than *E. cruciger* as a whole. It should be noted that these methods can only test the value of a proposed segregation; they do not suggest how the segregation should be made. For this one has to rely on the ordinary taxonomic procedure.

The last problem which will be discussed is the relation of taxonomic analysis to genetics. It may be said, in general, that there is only one way to obtain genetical information, viz. by conducting breeding experiments. In so far as taxonomists are forced to deal with genetically unanalysed material their conclusions on many points are open to criticism. The two main types of genetical information that are required to supplement the normal phenotypic analysis of taxonomists are, first, whether the characters studied are fluctuations or are genotypically determined (at least mainly); second, whether two similar looking variants (e.g. two melanic variants) are really produced by the same gene-combinations. Information of the first type is obviously fundamental, but more or less satisfactory indirect evidence bearing on this point is often obtainable. Without information of the second type, very erroneous generalizations might be built up, based on the geographical distribution, &c., of variants which merely *looked* similar. On the other hand, many animals are extremely difficult to breed in captivity, and in any case there is no hope that more than a few of the very numerous known species of animals can be investigated genetically.

It may be held that taxonomic data are singularly open to reproach in the absence of genetical information about most species. Such reproach is probably justified when well marked, 'qualitative' varieties are used as the material for generalization, but the case of metrical characters appears to be different. The absolute size of an animal, for example, usually seems to be affected by many genes as well as by the environment. It is probably nearly always impossible to analyse the genetic basis determining a particular size, though the extent to which the local environment affects the size of the individuals of a par-

ticular population can be demonstrated. With many metrical characters, therefore, particularly if they are studied in uniformly spread species and not in races living in widely separated habitats, it can safely be predicted that a considerable part of the variation is genotypic, and that the taxonomic and biometrical method of study is at least as effective as the genetic, for the latter is quite likely to involve an impossibly large amount of experiment.

It may be concluded, therefore, that as more attention is paid to metrical characters, genetical investigations lose their outstanding importance, except in determining the grosser effects of the external environment. It is true that in the latter question there is no completely satisfactory substitute for the direct experiment of rearing the race or species under controlled conditions. But there are certain methods of obtaining indirect evidence which might be more often employed than they are. When well-labelled specimens are available from different localities it may be possible to demonstrate that particular environmental factors, at any rate, can hardly have been of much importance. In the same way, specimens captured at different times of the year or in different years may enable one to learn something about the effects of climate on structure; climatic data sufficiently accurate for such preliminary investigations are recorded at a great many stations. In general it may be possible to correlate any metrical character of an organism with any metrical feature of the environment. Such correlations have for instance been widely established in various fish, but parallel observations on terrestrial animals have much less often been made; the honey-bee (Alpatov) being one well-investigated species.

Probably with most species we shall have to resign ourselves to correlating variation with environmental conditions without ever knowing whether two individuals of the same appearance are genetically similar. As long as the limitations of information of this sort are clearly realized, it still has considerable value. It is important to show that a given development of a character is associated with a particular type of environment or else that equal development of a character may occur under widely different conditions, even if the gene-basis of the character is unknown. For investigating many (not all) evolutionary

problems, the 'expression' of a character is more important than its genetic basis. For example, if a certain minimum size were supposed to be advantageous in dealing with some enemy, it might not much matter to the animal by what gene-combination that size was reached; the frequency of specimens of different sizes in various localities could be demonstrated without employing genetical methods.

It would be possible to make a number of further suggestions as to the uses to which quantitative taxonomic data could be put, but until it is more generally recognized that such data (when properly recorded) have a special value, it is difficult to try out any suggestion on a large enough scale to be conclusive.

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HUMAN EVOLUTION AND THE CONTROL OF ITS FUTURE

By A. M. CARR-SAUNDERS

IN very early days farmers must have become aware that it does not pay to spend more than a certain amount of labour on a given area of land, though this experience was not generalized as the law of decreasing return until little more than a century ago. So, too, stock-breeders in far-off days must have realized that the best results are achieved by selecting the parents with care. But in this latter case the experience of practical men was taken up and made the basis, not merely of the generalization that like tends to produce like, but also of a social programme. The interest of Greek thinkers in what has now come to be known as eugenics is familiar, and when proposing that human matings should be controlled, they pointed to the experience of the breeders of animals. But eugenics had not come to stay. As Greek civilization declined, the eugenic ideal was forgotten, and for more than a thousand years nothing more was heard of the matter.

Eugenics was next mentioned in the sixteenth century, but its reappearance in the writings of More and Campanella owed nothing to the rebirth of the practice of original observation. Its mention in their works takes the form of an echo of Greek thought, and did nothing to create an enduring interest in the subject. It is to the renaissance of science that renewed attention, which is likely to remain permanent, is due. It was some time, however, before the rebirth of science had this effect. If we place the rise of modern science in the middle of the sixteenth century, we find that the idea of improving human stock was not advanced until after more than three hundred years of scientific progress. During all this time neither biological research nor the experience of practical men brought the idea to light. It is more remarkable that the resounding successes of the improvers of farm animals—the work of Bakewell on sheep and cattle, for example—and the great interest with which their work was followed should not have

led to the rebirth of eugenics than that scientific progress should have failed to do so. For the prevalence of the notion that species were fixed tended to inhibit the idea of biological change. To the unpreparedness of biologists to grasp the idea must be added the fact that the prevailing religious conceptions were not of a character which made its emergence easy. In any case, however we may explain the long delay, it is a fact that eugenics was not reborn until after the publication of the *Origin of Species*.

It is well known that Darwin was extremely cautious in drawing any conclusions from his study of the problem of species to the case of man. He merely says that 'light will be thrown upon the origin of man and his history'. Twelve years later he dealt very fully with the history of man, but his reference to future possibilities was brief. He remarks that, although 'man scans with scrupulous care the character and pedigree of his horses, cattle, and dogs, before he matches them', 'he rarely, or never, takes any such care' in his own case. 'Yet he might by selection do something not only for the bodily constitution and frame of his offspring, but for their intellectual and moral qualities.' With a few more remarks of a general kind and a reference to Galton, that is all he had to say in *The Descent of Man*. He does not seem to have returned to the subject in any later publication.

The reference to Galton is significant, for it is to him that we must attribute such interest as was displayed by Darwin in eugenics. In 1865, six years after the appearance of the *Origin of Species* and six years before that of *The Descent of Man*, Galton published an article the object of which was to demonstrate the inheritance of mental qualities in man. In 1869 he worked up his material into a book entitled *Hereditary Genius*. Thenceforward he devoted his great abilities chiefly to problems relating to inheritance; and, since there will be something to be said later by way of criticism of the deductions he drew from his work and of the propaganda which he initiated, it should be made clear that no informed person would wish to belittle Galton's claim to be a great man of science. But he was also a propagandist. While his scientific labours were continued without a break, his propagandist activities in favour of eugenics, which began in 1865, were little in evidence

between 1880 and 1901. Thenceforward until his death in 1911 he was actively engaged in attempting to popularize eugenics. It is necessary to say something about this aspect of his work because the form which it assumed has left its imprint on the eugenic movement up to the present day and still governs the prospects of initiating any eugenic policy.

In the paper published in 1865 to which reference has been made, Galton showed himself to be extraordinarily sanguine concerning the possibilities of controlled breeding. 'The power of man over animal life,' he wrote, 'in producing whatever varieties of form he pleases, is enormously great. It would seem as though the physical structure of future generations was almost as plastic as clay, under the control of the breeder's will.' Later (in 1883) he wrote that 'we greatly want a brief word to express the science of improving stock'. Ten years earlier he had used the term 'viriculture', which in 1883 he replaced by 'eugenics'. Eugenics was ultimately defined as 'the study of the agencies under social control that may improve or impair the racial qualities of future generations, either physically or mentally'. Thus Galton was seeking a name for his 'science' before the foundations of our modern knowledge of inheritance had been laid, that is to say at a time when men knew no more than the Greeks, namely that like tends to produce like. In a revealing letter to Bateson written in 1904, after saying that the aim is 'to increase the contributions of the more valuable classes of the population and to diminish the converse', he remarks that 'exact knowledge of the true principles of heredity would hardly help us in its practical solution'. His science was therefore explicitly based on rule of thumb. He then went on to define eugenics, as we have seen, in words which are inappropriate in the description of any science. Had he used the word 'change' instead of the words 'improve or impair', the definition would have been acceptable; but, by introducing the latter words, he imported concepts of value which are out of place in the description of a science.

Nor was this all. In various passages Galton assumed that the 'upper classes' possess better hereditary qualities than the 'lower classes', though he was more cautious in making this assertion than many of his followers. It is also clear that he attributed very little importance to environmental influences

although serious investigation of the problem had hardly begun. Added to all this he wrote about eugenics with an absence of humour and want of perspective that made the subject seem either ludicrous or repellent. In the paper of 1865 there is a sketch of a Utopia in which 'a system of competitive examination for girls, as well as for youths, had been so developed as to embrace every important quality of mind and body'. There was 'an annual ceremony' during which the 'Senior Trustee of the Endowment Fund' addressed 'ten deeply blushing young men, all twenty-five years old', and so on. In consequence eugenics, from the moment of its rebirth, became a target for criticism, not only by those who take the easy course of rousing public opinion against anything which can be made to appear cranky, but also by those who dislike proposals ostensibly based upon science when that basis is insecure.

Thus the story of Galton's undue haste, premature conclusions, and lack of judgement is not a mere curiosity of history. It has profoundly affected and still governs the standing and prospects of eugenics to-day. Biologists were shy of the movement, and many still remain so; cranks and ill-informed enthusiasts appeared as supporters. The growing number of persons interested in social reform were antagonized, while those taking part in the rising labour movement, who resented social inferiority, found themselves branded as biologically inferior. In other countries, to which the eugenic movement has spread, the situation is much the same. Nevertheless, no biologist who accepts the main elements of Darwin's teaching can doubt that there is a case for controlling human evolution. What is this case, and how under all the circumstances can any progress be made?

The general case for attempting control is based on the following considerations. Evolution is now seen to have been a process of genetic change. New species arise as the result of the accumulation within a group of individuals of a relatively large number of small units of difference more often than of a small number of large ones. In this way our ancestors came to differ from some ape-like form. But this process of change has led far more often to what we may fairly call degeneration than to progress; loss of organs and loss of functions have been much more common than gain, and indeed innumerable species have

become extinct. The danger of degeneration is especially great for a dominant species since intraspecific competition may lead to results which benefit the individual but are lethal for the species. Man is dominant as no species has ever been, and thus incurs this danger in an unusually acute form. This is the general case for conscious control. Therefore, if we wish to preserve our genetic heritage, upon which our dominant position rests, we must take thought and act accordingly; this is still more necessary if we wish to improve it. To this may be added the fact that there are now certain new and powerful agencies in Western civilization, working through differential reproduction rates, which are likely to bring about unfavourable changes.

This general case is not to be controverted by pointing out what is perfectly true, namely that, though we are apparently no better equipped genetically than were our ancestors of 30,000 years ago, we have made enormous advances and have 'improved' beyond all computation, owing to our faculty for profiting from the acquisitions of previous generations. For one thing there is no reason why we should rest content with our present genetic endowment. Much more important, however, is the undoubted fact that we are in danger of losing it. We shall only be deceiving ourselves if we fix our attention upon our achievements and neglect the capacities which have made them possible. If our capacities are not maintained at something like their present level, it may prove impossible not merely to improve but even to retain the acquisitions of past times. Nor is it any argument against the eugenic case to point out, what is also true, that civilization can fall and has fallen for reasons unconnected with genetic change. The point is that unfavourable genetic change can destroy not only the civilization of the time, but also the species itself, whereas lapses on the part of a society of reasonably well endowed beings can be repaired in the long run.

As soon as Darwin's conclusions had won general acceptance, that is some seventy years ago, it became possible to build up the case in some such terms as these. Galton's mistake was to encourage the belief that biology could at that time do more than provide a very rough guide to action in the form of the breeder's maxim that like tends to produce like. Galton also

failed to emphasize that there was then general ignorance as to the extent to which likeness may be the result of like experiences as well as of like genes, and that this problem is of peculiar difficulty and importance in the case of man. How does the matter stand now in the light of the advance of genetic research since that date?

It has now been established that inheritance in man as in other organisms is on Mendelian principles. What are the practical implications of this? Since we cannot control genetic segregation, it follows that we can influence the genetic constitution of the community only through deliberate selection. In other words the only procedure available for controlling human evolution is still that which was deduced from Darwin's labours and was advocated by Galton. But the elucidation of the mechanism of inheritance, begun by Mendel, has enabled such investigators as Haldane, Fisher, and Wright to calculate precisely what the effect of selection will be under certain circumstances—a matter of the first importance concerning which nothing was known until recently. If the type of inheritance is given and also the system of mating, we now know, thanks to these workers, what will be the result of a given intensity of selection. The simplest case is when selection preserves only a recessive type, under which circumstances all dominants are exterminated in a single generation. When selection favours a dominant type, the rate at which the recessive will be eliminated depends upon whether we are dealing with an autosomal or sex-linked gene. In the former case it has been shown that, if a recessive type with an incidence of 0·3 per cent. in the population is never able to breed, it will be reduced from 100 to 82·6 in the first generation, to 69·4 in the second, and to 59·2 in the third. The reduction becomes less in later generations. In the latter case selection is far more rapid; if a type dependent upon a recessive sex-linked gene were restrained from breeding, it would disappear among females in a single generation and its incidence would be halved in the other sex in each generation. Such calculations show what will happen when selection is at its maximum efficiency and where we are dealing with single genes. When selection is slow, when, for instance, one in a thousand more of one type (depending upon a single gene) die than of another,

3,000 generations are required to increase a dominant type from 5 to 50 per cent., and 5,000 generations in the case of a recessive type. The matter becomes still more complicated when we are dealing with a type dependent upon the co-incidence of several genes. It has been shown that selection takes far longer, when acting upon such a type, to produce a given effect than when a single gene is concerned.

The importance of knowledge of this kind is obvious. Formerly, though in fact nothing more was known than that selection does produce results, it was often assumed that selection was everywhere more or less equally effective. We now see that, in Hogben's words, 'we are not entitled to form a definite idea concerning the influence of selective agencies either as factors operating over comparatively short periods in the history of mankind or as instruments for moulding the future of the human race, unless we can define the mode of transmission of the genetic differences with which we are concerned'. In other words, until human beings have been subjected to genetic analysis, we cannot say with any precision what effects could be produced by selection. It is appropriate at this point to remember that investigation has revealed another important fact. So far we have been speaking of what could be done by selection acting upon the genetic material now available. We now know that changes are produced in this material from time to time by mutation. As yet we are unable to influence the rate or direction of mutation in human beings, though it seems likely that mutation is not uninfluenced by the surroundings. Therefore, except in so far as mutation produces something new upon which selection can act, our efforts are limited to doing our best with the present material.

The next matter of importance concerns the extent to which it has so far been possible to identify genes in the human species. A number have been made out. Whether the lobes of the ear are free or attached depends on a single gene difference. Albinism is due to a single recessive gene, while brachydactyly is due to a single dominant gene, and the same is apparently true of the presence of a white lock of hair in one region of the head. The blood groups are also inherited in a simple fashion. There are in addition a number of conditions of a clearly undesirable kind, such as Leber's disease, amaurotic

family idiocy, pseudo-hypertrophic muscular paralysis, and split foot, which are due to single genes. Though this list could be lengthened, exact knowledge 'of the mode of transmission of the genetic differences with which we are concerned' is at present very limited. Nevertheless it is possible to draw conclusions of some importance regarding other traits. A large amount of information has been collected concerning the inheritance of stature, and Fisher has shown that the results are explicable on the assumption that this trait is determined by the interaction of a large number of genes. The same is probably true of intelligence and of many other traits which are of profound importance from the point of view of the control of human evolution. These inferences are important because, so far as they prove to be well founded, it follows that the effect of selection upon such traits will be slow.

At this point we reach a problem which, when it took the form of Nature versus Nurture, led to much useless discussion. We now see it in a different light. Our attention is concentrated upon differences between individuals, and we realize that such differences may have their origin in differences in genetic endowment showing themselves in the same environment, or in differences in the surroundings impingeing upon the same genetic constitution. This problem is relevant because it is essential to discover, in regard to any differences between human beings in which we are interested, how far genetic unlikeness is responsible for them. Indeed, from the point of view of constructing a programme of action the solution of this problem is primary. We must first find out whether we are dealing with differences of a genetic kind; then we go on and attempt to elucidate the nature of the genetic differences discovered (whether due to single or multiple gene differences, and so on), and finally, when provided with this knowledge, we can hope to make precise statements about the effect of selection.

We may take some examples which illustrate how the matter stands to-day from the practical aspect. There are cases where the position is plain. Albinism, for example, is manifested whatever the surroundings, and we know that, when faced by such a trait, we are dealing with a single gene difference. Therefore we can say fairly precisely what should be

done if we want to increase or diminish the incidence of albinism by a given amount. But in the case of most traits which attract our special attention, such as intellectual differences (including mental defect), temperamental differences, and those relating to health and bodily vigour, the position is not so clear. For we find that some differences at least, in respect of such traits, can be produced by different surroundings and experiences. Thus the stature of children of given age has increased as compared with some years ago. We know that nutrition has improved, and since there is no reason for thinking that genetic changes leading to greater stature have recently taken place we are inclined to attribute the greater stature to improved diet. Why then should we not attribute all differences in stature to differences in the environment, and so also differences in intelligence, in temperament, and in social behaviour? May not tall people be merely those who have been best fed, and well-behaved people those who have been best brought up? There are several lines of attack upon problems of this nature. We can take the case where the genetic endowment is known to be the same but the environment is different, as exemplified in identical twins who have been separated soon after birth, and the case where the environment is similar but the endowment different, as when children are removed to orphanages at an early age. Another method is to study the relation between order of birth and the incidence of a particular trait which throws light upon the influence of the prenatal environment. Among other methods is the study of the incidence of cousin marriages among the parents of those exhibiting a particular trait which may bring to light the influence of uncommon recessive genes.

We may illustrate the use of two of these methods in regard to one important trait, namely mental deficiency. There is some evidence to show that mentally defective children are found preponderantly among the later-born members of the family. This must be because the environment of later-born children is less favourable. On the other hand the incidence of cousin marriage among parents of defectives is much higher than in the general population. This is only explicable on the assumption that recessive genes play a part in producing defect, and in fact leaves no doubt that genetic differences in

the shape of recessive genes are largely responsible for this trait. The study of identical twins leads to the conclusion that intelligence is little influenced by the environment whereas temperament is more affected. This method has yielded remarkable results in the hands of Lange, who studied several cases in which a criminal was one of a pair of twins. There were sixteen pairs of non-identical twins; in fifteen of these cases only one of the pair was a criminal. There were thirteen cases of identical twins; in ten of these cases both members of the pair were criminals. It is impossible to escape the conclusion that a particular genetic endowment has much to do with this particular form of anti-social behaviour.

It is not possible to do more here than to indicate the kind of methods available for attacking the problem of the origin of differences between individuals and the sort of conclusions to be derived from the use to which they have so far been put. Thus, while hair and eye colour are little influenced by the surroundings, stature is considerably influenced; nevertheless, there is no reason to doubt that a group of children, all adequately fed, would exhibit large differences in stature due to genetic differences which are almost certainly based on the coincidence of many genes. Similarly, while intelligence seems to be but little modifiable by the environment, temperament is more so; it appears that while obstinacy, impulsiveness, vanity, self-assertion, and their contraries are largely determined genetically, environment may decide how far an obstinate person obstinately pursues good or bad ends, and how far a vain person prides himself upon worthy or unworthy achievement. Persistent offenders are often both vain and obstinate, but a more fortunate environment might have given less anti-social outlets for the exhibition of their temperamental traits.

The general impression left by such studies as have been made so far may be summed up in Haldane's prophecy that 'the progress of biology in the next century will lead to a recognition of the innate inequality of man'. If men are innately unequal, it means that there is a great variety of genetic material upon which selection can act. We know the results which follow from selection of given intensity under given circumstances. Thus we have some idea of the kind of result

which might follow from the adverse selection which always threatens a dominant species and which now appears to be actively at work in Western civilization. The only consolation which we get from a contemplation of the present situation is derived from the fact that, when a trait is dependent upon multiple genes, selection produces results more slowly than when single genes are involved. This provides some consolation, because, as we have seen, there is good reason to suppose that some traits, to which we must attach much importance, such as intelligence, temperament, and bodily vigour, are dependent upon several genes. Therefore, the present adverse selection, even if fairly intense, may not be rapidly followed by such unfortunate consequences as might appear at first sight. But this is only to say that we have time in which to act. What therefore can be done, and what hope is there that it will be done?

About 1 per cent. of the population of this country is mentally defective, and perhaps one in 200 is afflicted with congenital blindness, deafness, or some other serious inborn defect. All such persons are a burden to others and many of them a burden to themselves. None of them can lead a full life. Quite apart from the question of the proportionate increase of such persons, it is a proper aim of any society to reduce the incidence of these afflictions. We know already a good deal about the mode of transmission of some of these conditions. Thus brachydactyly is due to a single dominant, Leber's hereditary optic atrophy to a sex-linked recessive, and juvenile amaurotic idiocy to an autosomal recessive. As we have seen, prohibition of breeding would eliminate the first condition in one generation, and would drastically reduce the second condition in two or three generations. The elimination of the third is a more difficult task, though it could be achieved in time if the parents of juvenile amaurotics were prevented from having more children, and if the brothers, sisters, uncles, and aunts of affected individuals were prevented either from reproducing or from having more children. Such mental defect as is congenital (and it appears to be largely of that character) probably depends upon a few recessive genes. Its elimination would therefore be a long and difficult process, but a fairly substantial reduction could be achieved in a century or so.

The case for action in regard to this 1·5 per cent. or thereabouts of the population is strong, and the action to be taken is to make breeding impossible: of the afflicted in all cases, and in some cases of relatives also. Since legal prohibition upon marriage is useless, sexual segregation and sterilization are the only available methods. Sterilization is at present illegal; there is a strong argument for changing the law, not, however, in order to enforce sterilization compulsorily, but to enable persons to be sterilized of their own free will. Compulsory sterilization would lead to all kinds of dangers, and among others to a loss of confidence in the medical profession, the members of which would be regarded by many people as inquisitors armed with the power of forcing an operation upon patients, who, unknown to themselves, were afflicted by some condition scheduled as appropriate for sterilization. Sterilization is merely an adjunct to segregation, but possibly it would prove in time to be a very useful and welcome adjunct.

The problem of dealing with the 1·5 per cent. of the population is difficult enough in the present state of public opinion. But it is simplicity itself compared with the difficulty of dealing with the remainder. This 98·5 per cent., or whatever the true proportion may be, is composed of persons all capable of leading lives of some usefulness. There is no case for attempting to eliminate any of them. On the other hand they vary enormously in their congenital endowments; very many of them are poorly endowed in respect of physical vigour (the basis of robust health), intelligence, family feeling (which is the foundation of altruism), curiosity, and of other desirable temperamental traits. It can hardly be doubted that this large and poorly endowed section would be unable to sustain our complex civilization or perhaps any civilization at all. But there is reason to believe that this section contributes a disproportionately large number of descendants to the next generation, while those with valuable gifts seem to leave behind them so few descendants that their children may not compose one-half of the fraction of the population which their parents formed of their generation.

The way of escape from the menace of biological degeneration has been opened out by the advent of birth control, perhaps the greatest revolution in all recorded history. Parent-

hood has become voluntary in the better-off section of the population; voluntary parenthood is spreading, and the chief obstacle to its spread throughout 99 per cent. of the population is the lack of a simple, effective, and cheap contraceptive. It is unlikely, however, that we shall have to wait long for an instrument of this nature. Experience has shown that, where parenthood is voluntary, people do not leave enough children to replace themselves. In other words, under a system of voluntary parenthood, there is a very real danger of extinction. There is no reason to suppose that the less well-endowed section of the population will be any less active in reducing the size of their families than the better-endowed, once a cheap, efficient, and simple contraceptive is available. Under these circumstances, those communities which are threatened by a decline in numbers and ultimate extinction will have to address themselves to the task of raising the birth-rate. Here comes the opportunity of taking the control of human evolution in hand. If somehow the less well-endowed continued to fail to replace themselves, while the better-endowed raised their birth-rate, things would begin to move in the right direction.

Given a system of universal voluntary parenthood, the objective is clear, though it may be hard to devise the means of achieving it. It is reasonable, however, to hope that there will in time be a certain tendency for differential fertility to work in a biologically favourable direction even in the absence of any definite measures. Those endowed with strong family feelings may be expected to have larger families than others when all families are voluntary, and family feeling is probably, as we have seen, the main congenital basis for altruism. It is rather less likely but still possible, especially as knowledge of biology spreads throughout the population, that those with unusually valuable traits, whether intellectual, temperamental, or physical, may desire more strongly than others to leave descendants behind them. Indeed, in the long run much may be expected from the growth of a eugenic conscience.

It is plain that Western countries will all soon be driven to devise measures definitely intended to increase the birth-rate. These measures may take various forms, but among them there is certain to be a grading of taxation in such fashion that it falls more lightly upon those with a number of dependent children

than upon others. It is almost equally certain that family allowances will be granted in one form or another. Developments of this kind may or may not be followed by favourable biological results. If the consequence of such measures is to encourage indiscriminate breeding, the results will not be favourable. But, unless the measures are unskilfully applied, the results are more likely to be good than bad; for the position which is disclosed by our present limited experience of the voluntary family is as follows. Families are kept very small for a variety of reasons, of which the three most important are the facts, first, that, since children are a tie, parents with young children must forgo many pleasures involving absence from home, and are in fact more or less slaves to their children; secondly, that pregnancy and child-bearing are highly uncomfortable, to put it no higher; and thirdly that, since income does not increase with the increase in the family, income per head is reduced with the advent of each child. It might be possible, though it would be very costly indeed, to equalize matters financially as between those with and those without children by means of family allowances. It would be possible to do something to mitigate the troubles of pregnancy by further medical research, and also to some extent to relieve the pressure upon parents by increasing such social services as make provision for home helps, crèches and the like. But, even with the fullest development of measures designed to raise the birth-rate that is at all likely in the next two generations, those undertaking to rear a family of moderate size will remain under marked disadvantages, both financial and personal, compared with the childless. If that is so, such measures as have been indicated will do no more than smooth the path to parenthood for those who want children. Under these circumstances indiscriminate breeding would probably not be encouraged, and all that would happen would be that those desiring children for unselfish reasons and for reasons that may be called eugenic would be less discouraged from having them than is the case at present.

Thus the eugenic aim may be achieved in time as part of a general population policy. It is not likely that substantial progress will be made as the result of propaganda along the present lines and under existing auspices. For eugenics is still

under a cloud owing to the unfortunate impression made by its first exponents and to the fact that its most vocal supporters at the present day continue to offend biologists and public alike by their way of presenting the eugenic case. It may be that it would be advantageous and in the true interests of eugenics to abandon the word—so strong are the unfortunate associations which have gathered round it.

The course of evolution 'has generally been downwards. The majority of species have degenerated or become extinct, or what is perhaps worse, have gradually lost many of their functions. The ancestors of oysters and barnacles had heads. Snakes have lost their limbs and penguins their power of flight. Man may just as easily lose his intelligence. . . . If, as appears to be the case at present in Europe and North America, the less intelligent of our species continue to breed more rapidly than the able, we shall probably go the way of the dodo and the kiwi. . . . It seems to me altogether probable', says J. B. S. Haldane in another place, 'that man will take this course unless he takes conscious control of his evolution within the next few thousand years.' All that need be said by way of comment is that 'hundreds' would be more appropriate than 'thousands'.

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ANIMAL NUMBERS AND ADAPTATION

By CHARLES ELTON

AT a time when ecology and genetics are each racing swiftly towards one new concept after another, yet with little contact of thought between the two subjects, there may be some advantage in surveying, if only synoptically and in a preliminary fashion, the largely uncharted territory between them. When Darwin wrote his works on the origin of species, he had a clear insight into the nature of the struggle for existence, which sprang from his wide acquaintance with natural plant and animal life gained on the voyaging in South America, and afterwards in the smaller world of garden and country-side that he lived in. But he had practically no certain material from which to build a reliable theory of variation, not even distinguishing between inherited and phenotypic.

During the twentieth century there has been sufficient growth of genetics to enable the general nature of variations to be determined, even if their causes are by no means always established. In spite of various discussions still raging down side-alleys, we can say that the subject of variations is fairly well understood by geneticists. But their training and experience prevent them from knowing much about the struggle for existence in nature, that is to say, the section of ecology which deals with animal populations, competition, and similar subjects. Ecologists, correspondingly, although they are being drawn into a deep study of numbers, have inclined to believe that evolution was long and ecology short, that variation and the formation of new races and species take place too seldom to be of much significance in ordinary ecological studies. Generally speaking, one of the assumptions made in most ecological work is that the species will remain constant. The best field studies of the species problem have usually been done by systematists, but their results have naturally lacked the experimental analysis of variation, or the background of population research which is needed in order to discover how these interesting systematic distributions may have arisen.

Interest in the spectacle of the natural cosmos, stimulated by men like von Humboldt, had encouraged a widespread dawning curiosity about the dynamic workings of the interrelations of animals and plants with each other and with their physical surroundings, which found its chief expression in Darwin's work in the middle of last century. We find in the succeeding years a brilliant and valuable expansion throughout the biological institutions of the world, of research upon the structure and classification of plants and animals, accompanied by a waning of active interest in natural conditions except along certain specialized lines of adaptation. The dazzling exhibition of this evolutionary pageant occupied zoologists, who were similarly absorbed in studying the equally fascinating patterns of morphological development.

Genetics was reborn at the beginning of this century, and animal ecology in a modern form soon afterwards; but for about twenty years animal ecologists followed chiefly the descriptive lines laid down by botanists in their study of plant communities, or else concentrated on the physiological relations of organisms to their physical surroundings. It is only since about 1920 that an intense upwelling of interest has taken place, often quite independently in different parts of the world, in the question of population dynamics. It comes from three sources chiefly: the logical development of studying community interrelations such as the food cycle, the fascination of this subject for certain pure mathematicians who have done much service in building up algebraic methods of expressing zoological phenomena in general terms, and the pressure of economic biological problems, so many of which hinge upon numbers and their fluctuations. We may perhaps compare this revival of interest in animal numbers during the last ten to fifteen years with the strides that genetics has made in chromosome research.

Three examples serve to illustrate the convergence between genetics and ecology which is an essential condition for a solution of the species problem. One of the most important recent monographs upon animal populations and their dynamics, by Gause [3], is called *The Struggle for Existence*, in order to draw attention to the place that competition between species should occupy in the study of zoology. The other example comes from genetics. Sturtevant and Dobzhansky have discovered that

wild populations of *Drosophila* are by no means pure stocks, but contain, in spite of external uniformity, a great many recessive genes, most of which would be partly or wholly lethal if they were present in homozygous pairs. This discovery opens up the possibility that wild animal populations contain as much individual variability as human ones; it may be compared with an analogous discovery that wild animal populations previously considered to provide the standard of good health for an overcrowded and diseased human race, are in reality just as much subject to diseases as man, indeed often in a more catastrophic epidemic form. With genetic complexity of a wild species must go much local variability in composition and the possibility of significant changes within the working life of a single investigator.

The third example concerns the mathematical techniques that are being gradually developed by geneticists for studying the spread of mutations, and by ecologists and epidemiologists for studying the spread of parasites and diseases. Both these subjects require mathematical methods for describing the chances of contact between individuals of a population under various circumstances. A mutation spreads by the mating of a male with a female. A parasite spreads by the meeting of one individual with another, or by the paths of individuals crossing, sometimes even by the same condition as with the gene: the contact of male with female. Movements and density equally affect both processes. It should be quite practicable to apply some of the present population techniques to the study of the fate of mutations; in this way a new significance would be given to the old idea that the germ plasm is parasitic upon its host, the body. In particular, the fast development of marking techniques designed to follow animal movements in the field and to allow of the estimation of absolute densities, offers important opportunities also for genetic analyses.

This preliminary sketch is to clear the ground for consideration of the probable relations between the spread of mutations and fluctuation in numbers. Fluctuations are a universal property of the network of plant and animal species populations that covers in a thin film the surface of most of the earth, and fills its waters. A first impression might be that every niche has long ago been filled with plants and animals dependent on plants, that the habitats are full to bursting-point with life.

This seems to have been in von Humboldt's mind when he wrote: 'wheresoever the eye of the naturalist turns, life or the germ of life lies spread before him.' The concept fits plant-life fairly well, but is not true of animals. It is obvious to any naturalist that the total quantity of animal life in any place is an extremely small proportion of the total quantity of plant life. This general observation has been amply confirmed by all recent studies of the biomass of animal species or animal communities. For example, the bird life on an acre of rich farm land with trees and hedges and grass and crops may be only a few kilograms in weight. The animal life is widespread, it has, so to speak, staked out its numerous claims, but seldom succeeded in exploiting them to the full. Only in certain intertidal communities of the sea do we feel that animals have reached the limits of the space that will hold them. Even here it is, cosmically speaking, a tiny film of life.

From this situation we may conclude that, on the whole, animal numbers seldom grow to the ultimate limit set by food-supply, and not often (except in some parts of the sea) to the limits of available space. This conclusion is also supported by the general experience of naturalists, that mass starvation of herbivorous animals is a comparatively rare event in nature, although it does occasionally happen, as with certain moth caterpillars that abound on oak trees in some years and may cause complete defoliation. With predatory animals it probably happens more often. If herbivorous animals often did reduce to this extent the margin of vegetation they would be obliterating their food-supply, and the cover which vegetation greatly affords them from their enemies, not to speak of the special microclimates and other conditions of life that it provides.

Fluctuations occur in every group of animals and in every habitat that has been investigated: an impression not derived solely from deliberate research upon fluctuating populations, since it has also been widely supported by ecologists studying populations for other purposes and from other points of view. These fluctuations are rather forcibly expressed in human affairs through the irregularity from year to year of pests, epidemics, and of various animal resources, notably in the sea. The idea that such fluctuations are due mainly to human interference may be dismissed as quite untenable. On the contrary it is we who are interfered with by them. We are also subject

to them ourselves. As examples of natural fluctuations that affect us directly may be mentioned: marine and freshwater fish—herring, haddock, salmon, whitefish; other marine animals—oysters, lobsters; other freshwater animals—crayfish, the fauna of reservoirs; fertilizing agents for fruit-tree blossom and clover—bumble bees, various flies; forest and crop pests—beetles, moths, aphids, and so on; fur-bearing animals—seals, rodents, carnivores; disease carriers such as mosquitoes and fleas, often in turn depending on other animal hosts which themselves (as rats) also fluctuate. These are familiar examples from a general phenomenon which is one of the main themes of the complex orchestration of animal communities.

Although the amplitude of fluctuation is often very great, scarcity alternating with high abundance every so many years, two things that we might expect do not often happen. The first, complete destruction of vegetation by herbivorous animals, has already been mentioned. The second is complete destruction over any wide area of either predators or prey. The factors controlling the limitation of these fluctuations are therefore of great interest, since they are the factors that critically affect the survival or extinction of species, that is, they partly control evolution. The occurrence of fluctuations gives us a rather different conception of extinction from that traditionally held by biologists. To approach extinction, at any rate locally, and often over very large areas also, is a common periodic fate of species. They seem to run so close to it that we cannot help feeling surprised that they do not more often reach it. We have to look, therefore, for conditions that are able in some way automatically to check either great over-increase or ultimate decrease to extinction, conditions that keep most species oscillating around an 'optimum' or average that is often quickly passed, on the way up or down. The older idea of a constant balance of nature, keeping numbers at a steady point, has been completely abandoned by ecologists. Nicholson [5] has, perhaps unfortunately, continued in his studies to use this word 'balance' for the mutual pressure between two populations, whether they are stationary or not. It is probably clearer, while the older conception still hangs in the air, to use Lotka's phrase 'moving equilibrium' for the fluctuation of two interrelated organisms.

A good deal of work has now been done on the mechanism

of fluctuation, especially that part which contains the predator-prey relationship. Mathematical theories of great complexity and general application have been already deduced by Lotka, Volterra, Bailey, and others. The form of equation that best satisfies the facts of nature has still to be settled, since in most instances the equations have run ahead of the facts and still await experimental or field testing. Broadly, there are two methods of treatment, which differ in essence, although they give somewhat the same results. Volterra and Lotka relate the reproductive rates of one species to the rates of increase of another, making one a certain function of the other. Bailey and Nicholson have developed a rather different line connected with the powers of search of predators for different densities of prey. Although each method has to make intensely artificial assumptions, the second is in some ways more close to nature. The results of such calculations are to show how difficult it is for the numbers of prey and predator (even in an isolated system of only two species) to balance without oscillation setting in. Mathematicians find in the bare facts of interaction a fundamental reason for fluctuation. This in turn may be changed or accentuated by external irregularities, as of climate or other species of animals. The interest of Gause's work is especially in his successful demonstration with simple biological models (two Protozoa competing, a predatory Protozoan and its prey, a Protozoan preying on yeast, a predatory mite and its prey) of the mathematical theories previously developed. We may say that Gause (also Chapman, with the flour weevil) has carried these ideas from the arm-chair to the laboratory. No one yet has applied them absolutely in the field, where conditions are so very much more complex.

Several important ideas can be gained from this work. If a predator is too efficient (that is either in its biological properties of increase, search, capture, and survival powers, or in having started with relatively high initial numbers) it may completely destroy the prey, its food-supply, and (at any rate in a small limited microcosm) die in its turn. Or, if the prey has some fairly impenetrable cover in which it can find sanctuary, the predator may reduce its food (i.e. the available prey) so far that there is too little to keep it going, and then die off. After this the prey can recover and in-

crease again, but then runs the danger of eating out (in the absence of control) its own food-supply and suffering reduction once again, perhaps catastrophically. A human example will show that this process takes place in the natural state, as well as in artificially maintained test-tube populations. The Indians of Quebec Peninsula have always lived on caribou, which they hunted with spears and other primitive means. Since fire-arms came into their hands, the herds have decreased, sometimes to the point of extinction. Normally, the Indians would in turn have died (as they have periodically here and there, when they failed to find the herds in certain years), but the white man's stores of food have kept them still alive. In one place, north-east Labrador, the deer retired to a fastness that few natives penetrated, and from here have made a recovery in numbers. The lesson from these examples seems to be that a permanent fluctuating system between a predator and its prey can only be kept going so long as the searching and escaping powers of each are safely balanced. It would seem, from general considerations, that as such 'armaments' evolved and became perfected, each new advance might make the system more unstable, and nearer the dangerous plunge to extinction.

There are two features especially that tend to preserve the prey from utter extinction. One is simply the scarcity itself, which makes searching by predators less efficient and less worth while as the scarcity grows greater. And as most wild predators have more than one source of food to draw upon, the scarcity of one species tends to drive them to live upon another not so scarce. The other important fact is the existence of cover, of places to hide from enemies. The structure of the earth's surface provides many forms of natural, geological cover, but usually we find this intermixed with organic material also, mostly from vegetation. Examples are the soil and partly organic silt. The vegetation itself affords an enormously vital type of protective cover. The existence of so much cover greatly increases the chances of a species escaping from its enemies, and makes a form of natural sanctuary, and increases the scarcity of *available* preys for predators (or for parasites searching to lay their eggs in insects, or for organisms of disease). The various strange devices that animals have evolved for escaping detection, by special resemblances to their en-

vironment, and the opposite type of device that warns the enemy that he is approaching some food he will not like, and the various forms of bluff that have grown from these devices, are all part of a more general problem of cover.

This brings us to the consideration of how fluctuations affect evolution, if they do. It seems hardly possible that such a deeply rooted feature of the natural communities can be without considerable effect on the origin of races and species. But little has yet been done to clear up the matter or suggest just how it may affect the process of change. We may study the question in two stages. First, how do fluctuations affect the spreading of mutations? Secondly, how do they affect adaptation?

These two processes are not necessarily the same, although they were mostly thought to be in the older philosophies, and there is a strong school of geneticists who believe that every gene must have influence upon the viability of an organism, and that therefore every spread of a gene must be accomplished by natural selection. This is still a very dark field, and one can only preserve an open mind about it until some further facts collect.

There are several very solid difficulties about the origin of species that have gradually become clear. One is that closely allied species do not seem to differ in ecologically adaptive characters. No one has yet explained in a satisfactory way this anomaly. It suggests that mutations can spread without being ecologically advantageous to the species, a conclusion rather supported by the studies of Sturtevant and Dobzhansky [1] already mentioned, showing that natural populations may contain many sub-lethal factors. Another fact is that mutation rates do not seem to be sufficient to account, without discriminative spread, for the origin of such features in species. Another rather curious thing is that in spite of frequent reduction of populations to low points of numbers the species should not have become particularly pure genotypically. Finally, it seems to be fairly well admitted that a large number of mutations are of a type that could not, without some transformation, be made even into harmless but useless ones. On the last point, we have, however, several ingenious experiments and theories which claim with some justification to show that such harmful mutants may develop good qualities, through sorting of their companion genes.

The idea that mutant individuals may occasionally be preserved during a low period of fluctuating numbers has been suggested by me and analysed, with adverse result, by Haldane [4]. He comes to the conclusion that the chance of a mutation becoming established by chance in such a way is too remote to be of practical significance. The calculation may require revision in the light of the undoubted fact that reduction in numbers takes place patchily, and not in a uniformly distributed manner. We might imagine, for instance, a melanic squirrel mutant, arising or preserved among a few normals during a low period of numbers, expanding in numbers for several years to provide a large number of descendants black or carrying blackness, then surviving another epidemic without heavy loss, owing perhaps to comparative isolation of the stock in a particular wood, from which this nucleus could colonize neighbouring areas now largely depleted of normal animals. This sort of process might not happen very often, but when it did the result would perhaps be crucial. And new races are not established very often. With such a basis, local accumulations of new mutant strains could arise, to form the material on which natural selection or other processes could act. There is no way in which we can calculate the probability of this process taking place for a particular species or a particular mutation. The only way in which the matter can be carried further is to undertake marking experiments on various mixed populations on a large scale in the field, and follow their fate through several cycles of increase and decrease. Until this has been done, the matter cannot be considered as closed. The fact that mathematical calculations about field populations are at present limited very closely by their framework of assumptions, e.g. about random distribution, and that there are many irregular field phenomena that cannot be treated theoretically, is often forgotten.

We pass on to the next stage, in which we assume that a new element has already spread to some extent in the population (whether by natural selection or by chance). We wish to know what effect it will have upon oscillations in numbers and how the oscillations will affect its spread, i.e. its fate as a variety. A. J. Nicholson has made the first approach towards this problem in several analyses chiefly concerned with the particular example of insects, their predators and parasites, but also to

some extent from a general point of view. He points out the important conclusion that adaptation does not necessarily increase the numbers of a species on a given area. Suppose we take the example of an insect with a concealing pattern that increases its chance of escaping from a bird or lizard predator. It is also attacked by parasites (i.e. insect predatory parasitoids) with which it lives in a state of moving equilibrium, with oscillations. There is a mutant which favours concealment. More insects than usual escape the birds and lizards. The numbers rise more quickly than usual, perhaps to an abnormally high level if there is a lag between the insect and its parasites. There is unusually heavy infestation of the host population, and this brings them down very low, after which, with host scarce and parasites less able to find them, the host numbers start to climb again. This process Huxley has named 'intraspecific selection', and Haldane has discussed it in relation to similar processes that occur in plants. The same result would happen if the new mutant speeded up reproduction or growth, so that dilution of the slower forms would gradually occur. The process might occupy many cycles of the fluctuation before equilibrium was once more attained.

The principle of this process is that a specific adaptation causes an increase to higher density, and that then another factor that does not discriminate between the old and new adaptation reduces the whole population, perhaps somewhat catastrophically (though not necessarily so) to a lower level. The idea is familiar in other fields. The prevention of human deaths at birth may cause increase which brings in train famine or new disease for adults. The deer in a conservation park is freed from its 'enemies' and overeats its vegetation food reserve in winter, and begins to starve, and is worse off temporarily than before. Were it not for the sudden action of disease or of unfavourable weather conditions at a time of dearth, the whole population might become extinct from starvation, or so low that it could not surmount the normal toll that every species shows in its physiological death curve.

There is, therefore, room to speculate whether moderate efficiency in certain adaptations is not in the long run more likely to preserve the species than what is usually described as a 'beautiful' adaptation. A successful new mutation may spread because it is favoured in intraspecific competition. It

may, however, set up oscillations that become too high and low, leading the population near the margin of extinction. It may be found that there is such a thing as biological modesty that has a survival value, that the predator-prey or parasite-prey systems with most chances of endurance are those in which efficiency is equally matched, and in which neither is too highly developed.

There are, however, certain other considerations that come in here. One is that populations are seldom confined in a bounded habitat from which they have no escape. Migration is a common phenomenon and often takes place just when population pressure is greatest. With migration we get two types of spread: into the same habitat on a new area; and into new habitats. When a species makes these transfers of population, new limiting factors come into action, and change the situation.

Since there are as yet so few real facts on which to build a bridge between ecology and genetics, one can do little more than indicate the type of problem that requires solution. From these remarks it will be seen that fluctuation is such a deeply ingrained feature of animal populations that it must have some important effect on evolution, whether by favouring non-adaptive spread or by working with natural selection. And it is at least quite possible that mutation increases oscillations and that immediate gains may be lost by this very effect. The whole of population research is full of inversions and paradoxes, and the ecologist is becoming quite used to expecting the opposite of what might appear the obvious result. It is therefore not at all impossible that extreme adaptation, by favouring periodic higher densities, may bring about the extinction of a species, in much the same way that the highly developed efficiency of the human race at present makes its survival at continued higher density at any rate in doubt.

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CHANGE AND CHOICE: A STUDY IN PELAGIC ECOLOGY

By A. C. HARDY

ONCE a seed has germinated the resulting plant remains rooted in one spot at the mercy of its environment; but an animal possessing the power of locomotion has the opportunity for a choice of habitat.

If selection is a factor of importance in the evolution of a race, and the environment, both physical and animate, is the selector, then the fact that the individual has some power of choosing its own environment must be of consequence in the evolutionary process. In the evolution of motile animals there are two opposing selections at work. In the words of Elton [5], who has most forcibly brought his conception forward, there is 'the selection of the environment by the animal as opposed to the natural selection of the animal by the environment'.

As with rooted plants, it is clear that choice of environment can play no part in the evolution of sessile animals, except in their larval stages; but what of those representatives of nearly all the phyla of the animal kingdom, which inhabit the most extensive zone of life we know of: the vast collection of animals in the marine plankton? They have been defined by that expressive Greek word as 'those which are drifted'; it is used for all the animals which have not the power to migrate against the ocean currents. They are generally considered to be drifting passively with their surroundings, with no choice in the matter. The purpose of this essay is to re-examine the relation of these animals to their environment and to consider its significance in the evolutionary process.

In studying the marine plankton we are working with one great handicap compared with our colleagues on the land: we have to explore a hidden world, and only by groping in the dark can we attempt bit by bit to piece together a conception of its inhabitants and their behaviour. There is another difference: our field of work is more noticeably three-dimensional than that of the land ecologist who can usually consider his

animal and plant communities in plan, already distributed on the earth's surface as a two-dimensional map. In the sea we must never think only in terms of plan; our environment has depth as well as breadth. Different strata have different properties and travel at different speeds, and water masses may rise and fall.

While we have these difficulties in dealing with our unseen three-dimensional world, we have one great advantage: we are dealing with a fluid environment. By lowering thermometers, photo-electric cells, and water-sampling bottles to different depths we can build up an accurate picture of the surroundings. How difficult in comparison must be the assessment of the terrestrial habitat. The animals and plants too are more easily sampled by being strained off from the fluid medium in which they are suspended. By using standard nets in a uniform manner we can make comparative estimates of the population in any part of our environment. After such a net has been towed at a particular depth we can close its mouth by a special mechanism and so be certain that all the animals in it have come from that level and have not been caught on the way up to the surface.

An unusually intensive plankton survey was carried out on the antarctic whaling-grounds round the island of South Georgia in the southern summer of 1926–7 during the *Discovery* investigations under the leadership of Dr. Stanley Kemp, F.R.S. While the R.R.S. *Discovery II* has since carried out many more extensive surveys, none has yet been worked out in such detail as this which was intended to form an introduction to the ecology of the southern plankton community as a whole. The results [6], worked out jointly with Mr. E. R. Gunther, could not be published till eight years after the ship's return. The data to which I shall refer will be found fully set out in that volume of the *Discovery Reports*; but they have not before been discussed in relation to the evolutionary process.

The Royal Research Ship *Discovery* and her smaller attendant ship the R.R.S. *William Scoresby* worked together making lines of observations running out from the coast in all directions; along each line we stopped every ten miles to sample the sea and its life until we had reached out over water with a depth of a 1,000 metres or more. In addition we took stations

at one or two positions intermediate between each of these radiating lines. At each position the same standard routine was followed. Temperatures and samples of water for chemical analysis were taken at short intervals from the surface downwards; the smaller and larger forms of planktonic life were sampled with closing nets of various mesh, hauled both vertically and horizontally at different depths. In the end we had over a thousand of these plankton samples on which to base our conclusions.

Such a survey, in addition to telling us which were the more important species in the community and their relative abundance or in giving us a chart of distribution for comparison with later surveys, provides us with something more. No matter what the particular distribution is, and we know it must be soon altered by the flow of ocean currents, the study of the component elements of the community at any one time, in correlation with the various environmental factors, is of value in revealing something of the comparative behaviour of the different animals. It is with this behaviour and its significance that we are here concerned.

The more we explore the pelagic world the more widespread appears to be the remarkable phenomenon of diurnal vertical migration. The animals sink away from the surface in the day-time and climb towards it at night. This curious behaviour of planktonic animals has long been noted and the extensive pioneer investigations by Mr. F. S. Russell of the Plymouth laboratory are well known. He has studied the vertical movements of the animals by taking series of horizontal tow-net hauls with a standard net at different depths at different times during twenty-four hours at one place. Whilst we made some observations in a somewhat similar manner, the greater part of our evidence was obtained differently.

We carried out our survey continuously, steaming from one station to another, day and night, so that we were provided with a large number of observations taken at different places in the area but taken at all hours of the day. By disregarding the fact that they were taken on different days we can arrange the observations in a sequence through the round of the clock. Let us take one of our results in detail by way of example. In Fig. 1. we have prepared a chart of the occurrence of one

species of copepod, *Clausocalanus laticeps*, as shown by a series of three nets towed horizontally at each station at 5 metres and at two lower depths which were usually about 60 and 120 metres but varied considerably. It was impossible in the heavy weather we experienced to adjust the speed of the ship with precision, for the old *Discovery* was heavily rigged and had only auxiliary steam; but by placing Kelvin sounding tubes at the end of the line we could determine the depth at which the nets were fishing each time. Along the top of the chart is a time scale in hours from noon to midnight and to noon again. Along this scale are marked off the positions of each station in the survey according to the time of day it was taken. That part of the chart lying between sunset and sunrise is shaded to represent the period of darkness. Down the left of the chart is a scale of depth in metres. The position of each net haul, in relation both to depth and time of day, is shown as either a number representing the *Clausocalanus* taken or as a dot indicating that none was present. Disregarding occurrences of less than 50 as being insignificant, we have placed a circle round the sample giving the highest number at each station. We see how the position of greatest abundance gradually rises to the surface at night and falls away again at the approach of dawn.

This method has the advantage of presenting a generalized picture of the typical behaviour of the different species based upon a large number of different days and different places. A number of other examples of the method are shown in reduced and simplified form in Fig. 2; here only the samples with the highest numbers are put in at each station as filled-in circles or other symbols. We see clearly that the behaviour of the different animals is varied greatly to meet different conditions, otherwise the distribution of the greatest numbers would represent a more regular curve. Thus we studied the diurnal depth distribution of each species which occurred in sufficient number for treatment. Out of twenty-four such species all, with the exception of three copepods and possibly one species of chaetognath, showed evidence of vertical migration. In addition we employed two other methods making use of vertical net hauls which gave a good confirmation of the other results. Mackintosh [11], working on the plankton of later surveys over a wider area, has added many more species to

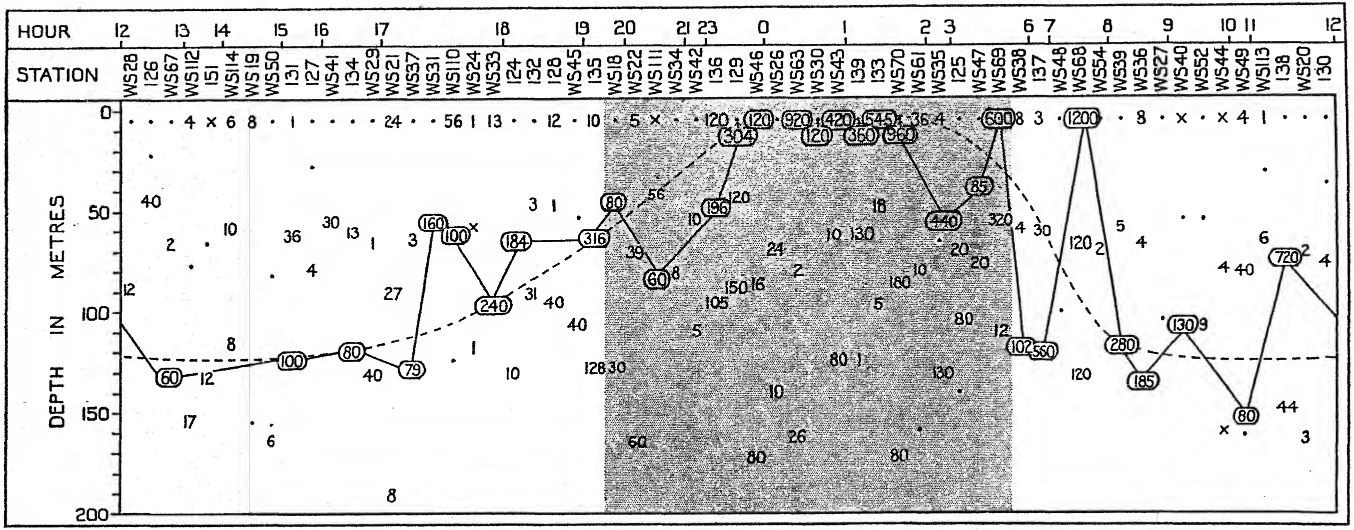


FIG. 1. The vertical distribution of the copepod *Clausocalanus laticeps* Farran, in relation to the time of day, based on the catches of horizontal tow-net hauls at different depths at each station in the South Georgia area. The position of each net haul in relation to the vertical depth-scale is shown as either a dot indicating the absence of this copepod or a figure representing the number caught. Where the highest catch at any station exceeds 50 this number is encircled. The stations are arranged from left to right in order of the time of day from noon through the night to noon again; the period between sunset and sunrise is shaded. The highest catches are connected by lines which are only significant in indicating the general trend of the diurnal vertical migration which is shown by the broken-line curve. From Hardy and Gunther (1935).

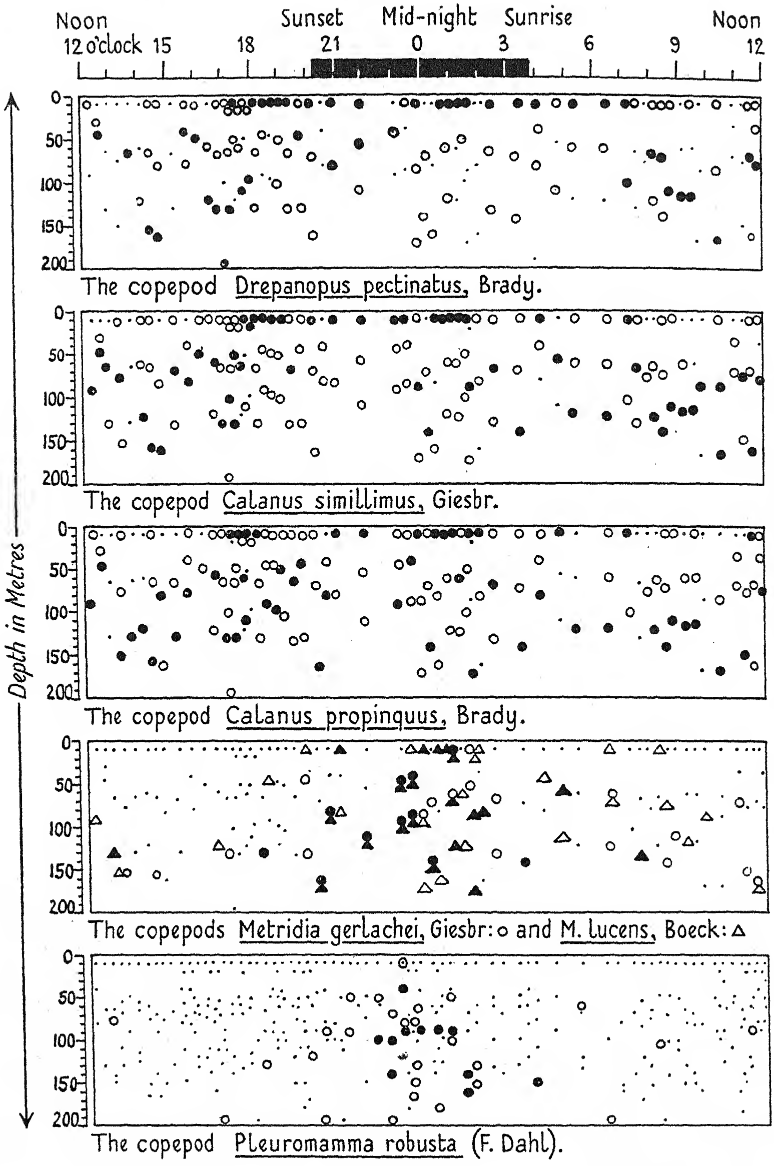
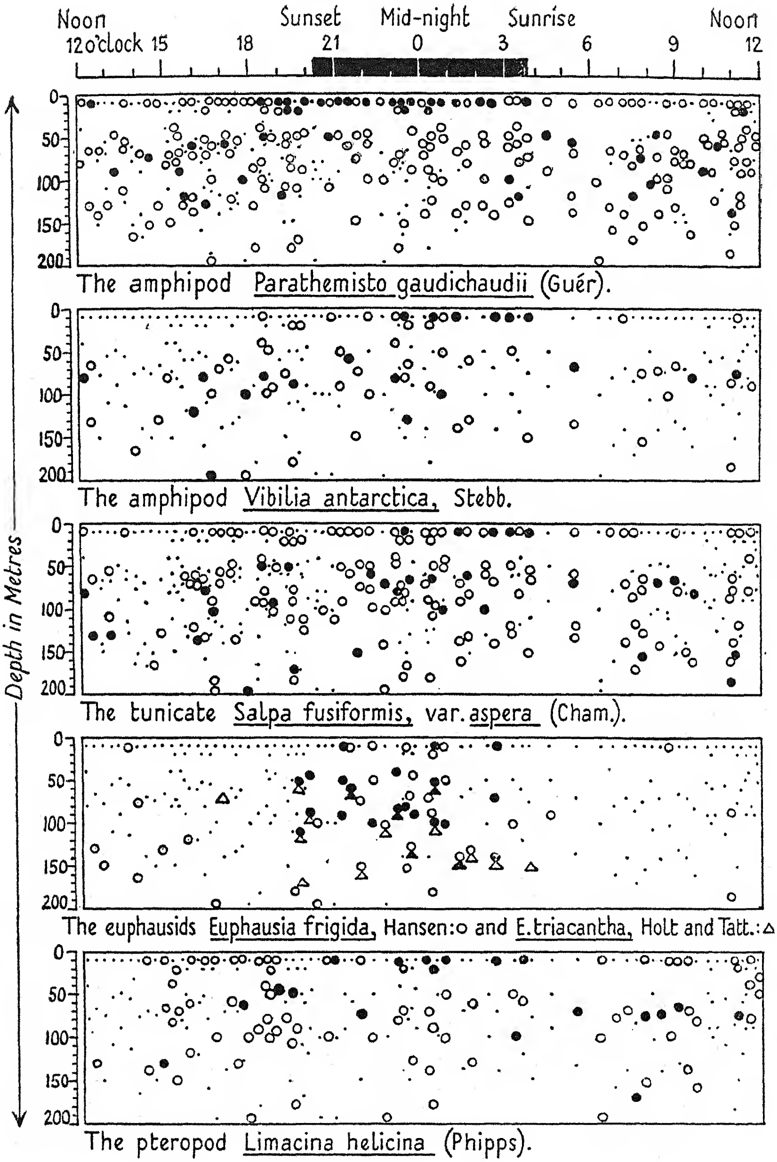


FIG. 2. Vertical distribution of plankton animals in the South Georgia area shown in relation to time of day, arrangement as in Fig. 1, but simplified (see explanation below Fig. 1). The presence of a particular species at each depth is shown as a circle (or triangle), its absence as a dot. Filled-in circles (or triangles)



represent the largest catch at each station (where this exceeds 50) or in the cases of *Metridia*, *Pleuromamma*, and *Euphausia*, all catches over 50. Redrawn in simplified form from Hardy and Gunther (1935), where full details will be found.

the list of animals in the antarctic community which show marked diurnal differences in depth distribution.

Medusae, siphonophores, chaetognaths and polychaete worms, crustacea of many groups, pteropods and pelagic tunicates: they all show the same general type of behaviour. The range of vertical migration of different species may be very different, and many of them climb hundreds of feet each day. The charts for such forms as *Euphausia triacantha* and *E. frigida*, or the copepods *Metridia gerlachei*, *M. lucens*, or *Pleuromamma robusta*, show that as soon as darkness has fallen these little animals have risen from below 170 metres, and sometimes the whole 500 feet to the surface, in a very short space of time. The copepods are but a tenth of an inch in length.

Such results may make one wonder whether the effects observed are really due to vertical migration at all or simply to an avoidance of the net by the animals in daylight. The latter interpretation can readily be disproved. If the animals were not going up and down then we should get as many in the lower strata at night as in the day-time; actually we see that there are usually fewer below as the numbers increase above, as in Fig. 1.

That this type of behaviour is so widespread in the pelagic world, that it should have been evolved independently in at least seven different Phyla, and that it should involve the expenditure of so much energy would seem to indicate that it is an element in the relation of the animal to its environment of exceptional importance. There can be no doubt that the movements of the animals are in part a response to light. The phototaxes of plankton animals have long been known. Russell believes that each animal prefers a particular light intensity: if the light increases the animal will descend till it reaches its optimum; if the light fades the animal rises. Experiments made by Clarke [2] at Cambridge, however, demonstrated that under laboratory conditions the freshwater *Daphnia* would respond to changing rate of intensity rather than to actual intensity itself.

All those who study vertical migration in the field know well that the same species does not always behave in the same way in relation to light. On some nights the animals will come to the surface, on others they will not come so high;

sometimes in the day-time they will go deeper than at other times. There are occasions when animals which are usually deep down in the day-time may be taken at the surface in strong sunlight. Our charts show that all the members of one species are not up together at one time; some remain down while others climb to the surface.

Many years ago Jacques Loeb [9] showed that copepods which were negatively phototropic could be made positively phototropic by reducing the alkalinity of the environment.

In the *Discovery Report* on the South Georgian plankton I have suggested an hypothesis of animal exclusion which I have linked with the phenomenon of vertical migration. Space will only permit the briefest reference to it. It has frequently been observed that when there is an unusual abundance of the plant plankton there is a scarcity of the animal members. Attention was first drawn to this in 1885 independently by two observers, Conte Castracane [1] and F. C. Pearcey [14], who took opposite views of its interpretation. The latter spoke of both herrings and animal plankton being *excluded* from regions of dense plant plankton. This inverse relationship was abundantly evident in our South Georgia survey, and it became apparent that it also held in a number of subsequent ones. It was possible to deduce correctly the whale distribution on a number of different occasions from the measurement of the phosphates contained in the upper layers of water: areas of reduced phosphates were found to indicate high plant production, and high plant production meant scarcity of Euphausians which were the food of the whales.

Harvey [7], as did Castracane, accounts for this inverse abundance of plants and animals by the simple explanation that the plants flourish in regions where the animals are scarce and that they are closely grazed down where the animals are plentiful. Undoubtedly the animals must often have this grazing effect, indeed every year the plant crop is being reduced by the animals as the summer advances. We, too, had distinct evidence of grazing effects in our survey. The two conceptions may be complementary rather than antagonistic. In the *Discovery Report* I have dwelt at length on the reasons for believing that grazing is not always the explanation of this

inverse correlationship. We see many different species of animal being distributed *together* away from the dense plant concentrations; some of these are numerically much more important in the community than others; the less numerous cannot have the same grazing effect on the plants as the more numerous. Why should all these animals have a similar distribution away from the rich plant plankton regions? Again, although through technical difficulties we have so far little knowledge of the actual species of diatoms usually eaten by the different animals, we should not expect the animals to be equally effective in grazing down quite different plant communities; yet we see the same animals having the same inverse distributional relationship with quite different plankton 'floras'. Further, apart from the inference drawn from numerous plankton surveys in the North Sea at the times of the fisheries [15], we have experimental evidence [8] that fish such as the herring *avoid* dense plant plankton areas—and they do this during part of the year when they are not feeding and so cannot be avoiding such dense areas because of an absence of their animal plankton food which might have led to the rich plant growth.

The inverse distribution cannot simply be due to the animals being killed off in the dense plant zones and multiplying in the other areas, because some of the animals with which we are dealing, e.g. *Euphausia superba*, are known to take two years to reach maturity, and the luxuriant plant productions are only transitory. If we accept it that this inverse distribution is not always due to the presence or absence of heavy grazing, then we must assume that the animals have the power of moving out of the dense plant plankton. They are too small to swim far in a horizontal direction; but they have the power of sinking away from the upper layers which are alone frequented by the plants. Now waters at different levels are nearly always travelling at different speeds. An animal going down from the surface and remaining at another level for a few hours will come up again to the surface *at a different place*. The longer it stays down, or the deeper it goes into waters having a more diverse speed from the surface layer, the farther it will be from its point of descent when once it rises again. Vertical migration provides the plankton animal, otherwise drifting at

the mercy of its environment, with the mechanism for *changing that environment for another.*

Briefly the apparent exclusion of animals from the regions of dense plant plankton seen in plan seems to be the result of an 'exclusion' in a vertical direction and an excursion into waters travelling at a different speed from the surface layer. I have retained the word 'exclusion' as that originally introduced by Pearcey, but the 'exclusion' effect is rarely complete; the numbers of animals in or below dense plant zones are merely reduced.[1]

Before passing to a closer examination of vertical migration as a means of enabling drifting animals to change their environment let us consider how in the first place it may have been caused. We see a marked difference between the two environments between which the animals migrate; there is a higher oxygen content and alkalinity, due to the carbon assimilation by the plants, in the upper photic layers.[2] It might seem likely that if not for this, then for some other reason, the animals find life in the lower layers the more congenial. Otherwise why should they not remain with their food-supply above instead of sinking to climb again with so much expended energy? Can it be that the lower layers are the more congenial because in the darkness below they escape attack more easily? The plants are abundant in a zone extending only a little way below the surface. At night the herbivores are accumulated densely in this narrow belt to feed; in the day-time they are scattered more widely through the deeper layers. Concentrated in the narrow plant zone they must present better feeding opportunities to the carnivores. Thus perhaps the herbivores climb to feed under the cover of darkness and the carnivores follow them, for the latter migrate as much as do the former. Against this explanation, perhaps, we must remember that many herbivores, for example the Euphausians, make themselves conspicuous at night by their luminescence. If the plant crop is dense they would be able to get sufficient food in a shorter time than if it is scarce and so return more quickly to the layers

[1] Nielsen [13] has recently suggested another hypothesis which may apply in special cases, but does not account for the facts observed in our survey.

[2] There are also slight diurnal differences in the oxygen content and the alkalinity in the surface layer itself because the photosynthetic activity of the plants is restricted to daylight; this difference, however, seems too small to be significant.

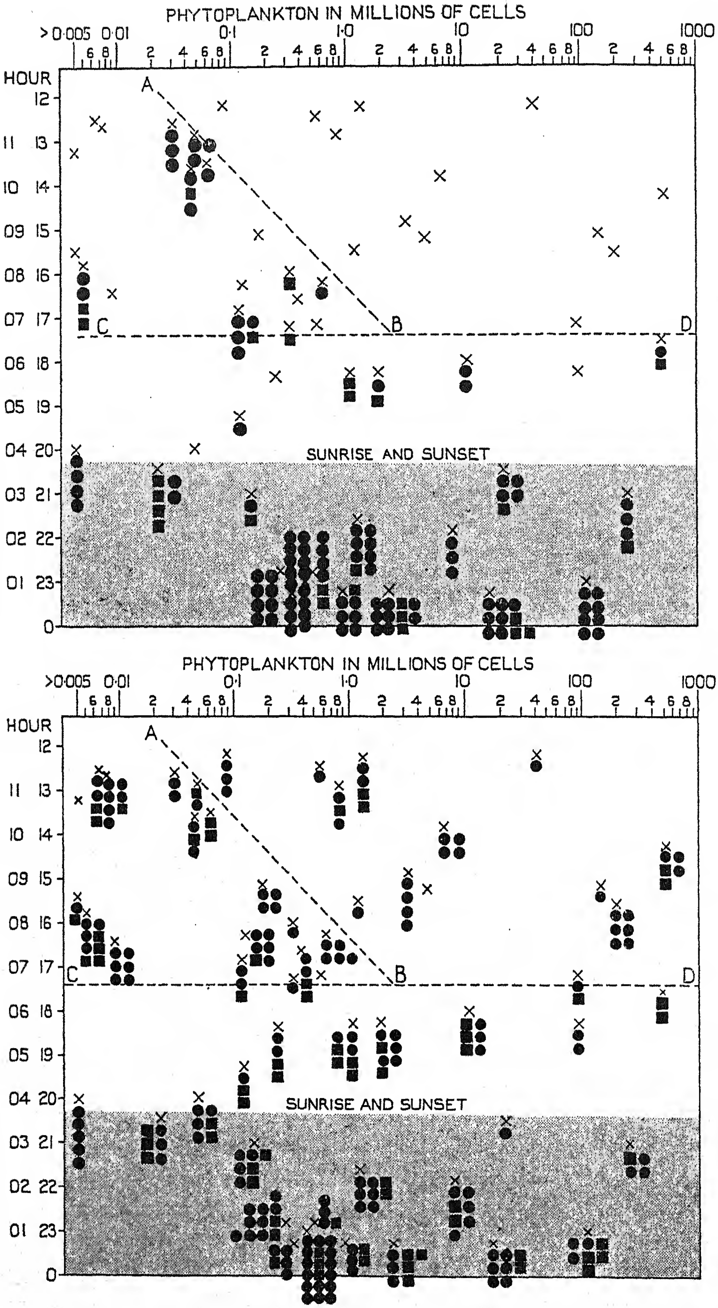


FIG. 3. For explanation see text.

below whatever might be the cause for their being the more congenial. The poorer the plant crop the longer the animals would have to remain in the upper layers to obtain sufficient food (and, it may be noted, the less would be the contrast in oxygen content and alkalinity between the upper and lower layers).

Clarke [3], experimenting further with *Daphnia*, made a discovery which perhaps may be of much significance in this connexion. Young *Daphnia* are positively phototactic, but as they become older their response becomes negative.[1] Now he found that if the culture medium gave out and the adult *Daphnia* lacked food, its normal negative reaction to the light became changed to a positive one. In nature it would have moved towards the surface into the plant zone.

There was some evidence in our survey that the animals did in fact tend to remain higher in the water in the day-time in the regions of poorer plant plankton. This is illustrated in the two charts in Fig. 3. Along the top of each chart is a scale of the plant plankton values found throughout the survey in millions of plant cells per unit haul, from very poor values on the left to very high values on the right. Up the side of each chart is a scale of time between midnight at the bottom and noon at the top; the hours of the day go up the scale 1, 2, 3, . . . to 12 noon and down the same scale 13, 14, 15, . . . to midnight. It is a scale ranging from darkness to noonday light; the area of darkness (between sunset and sunrise) is shaded. Now each station in the survey is plotted as an X in a position in relation both to time of day and to plant plankton density; stations occurring at say 8 o'clock in the morning and at 4 o'clock in the afternoon (16 o'clock) would be opposite the same point on the scale. The two charts are so far the same. Now the upper one is used to show the catches of animals in the *surface* nets and the lower one to show the catches of animals in the lower nets (100–50 metres depth). Against the position of each station there is placed a filled-in circle for each animal species of which over 100 were taken, and a square for those of which over 50 were taken. If the animals do remain at the surface

[1] It is generally the case that younger animals are higher in the water in the day-time than are the adults, perhaps because they require more food for growth and cannot afford the energy of a longer migration.

longer when the plant plankton is scarcer, then our entries on the upper chart should lie to the left of a diagonal drawn sloping to the right. This they largely do. In the area bounded by the line *ABC* there are eighteen stations at nine of which are found animals at the surface in numbers of over 50 or 100; in the area *ABD*, on the other hand, there are twelve stations at none of which are such numbers of animals found at the surface. The odds against this being a chance result are high. The lower figure shows that there were such numbers of animals at these stations *but lower in the water.*

It is noteworthy that *Euphausia superba* which showed the most marked 'exclusion' effects in our survey as seen in plan, should also give the most striking evidence of a day-time depth distribution modified in relation to the plant plankton. Using only the stations taken between the hours of 0800 and 1600 o'clock (approximately four hours after sunrise and before sunset respectively), and arranging them from left to right in ascending order of plant plankton values per standard unit haul, we see that its depth distribution as shown by the surface, middle (av. 59 metres), and lower (av. 115 metres) nets is as follows:

Surface net:	**160**	1	0	0	0	0	0	0	1	0
Middle net:	43	**678**	**554**	2	**264**	3	2	285	0	0
Lower net:	140	28	41	1	52	1	8	**521**	0	**179**

These field results are supported by experiments recently carried out in my laboratory by C. E. Lucas [10] who showed the animals with which he worked (Mysidae and the copepod *Eurytemora*) to be more photopositive in weak cultures of plant plankton than in strong cultures.

Vertical migration is a response to light which may be modified by other factors in the environment, and food may be only one of them.

It is important to remember that it is only in a vertical direction that these animals can usually detect a change in their surroundings. Even if they were able to move far to right or left they would usually have to go a relatively long way before they would find an appreciable change; so far indeed that unless they had a compass-like organ they would deviate from a straight line and as likely as not curve back towards their starting-point. In a vertical plane, light intensity will provide them with a means of judging the direction of their food-supply and

roughly their distance from it. Gravity may guide them down into the lower strata in the day-time, but diminishing light as they descend will prevent them going too far. As evening falls they will be guided back to the feeding-grounds as the light fades more and more. Those species which have a greater capacity for climbing may sink the deeper. This is the rising and falling optimum of Russell, though not a fixed optimum for each animal, but one varying from time to time with the animal's other relations with its environment.

Now let us return to consider more closely the effect of this vertical migration on this environmental relationship. If the

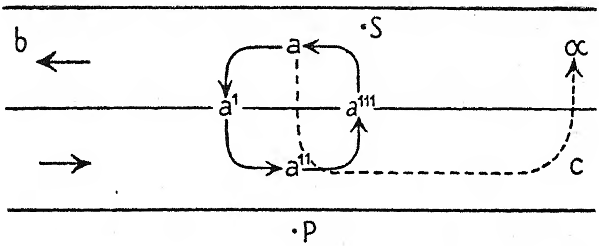


FIG. 4.
For explanation see Text.

sea were stagnant there might be little to say; but it is not, it is continually moving and different water layers are nearly always moving at different speeds and often in divergent directions. While the animal's movement appears to be modified by the plant plankton above, and one layer may well be more congenial than another, it is possible that the main virtue of the migration lies not so much in any difference between the vertically distributed environments, as in the consequences of the *movement* between them itself. Some examples will make clear what is meant.

Let us take in Fig. 4 the extreme instance of two water layers travelling in opposite directions at similar speeds; and from a position outside the system, say at P on the sea bottom, let us observe the path of an animal migrating between the two layers, going up at 6 o'clock in the evening and sinking at 6 o'clock in the morning. From a position a at midnight it will follow the path a', a'', a''' back to its starting-point. This is the starting-point in relation to the observer at P; it has not

come back to its original environment. The water which surrounded it when it started at *a* has now moved on to *b* and that which surrounded it at *a''* will have moved on to *c* by the time it is back again at that position in relation to *P*. If we had observed from a point moving with the surface layer at *S* we should have seen the animal follow the path from *a* to α.

We see at once that the vertically migrating plankton animals instead of simply drifting with one environment are continually being presented with a new one. The proposition just taken is admittedly an extreme one, although we shall

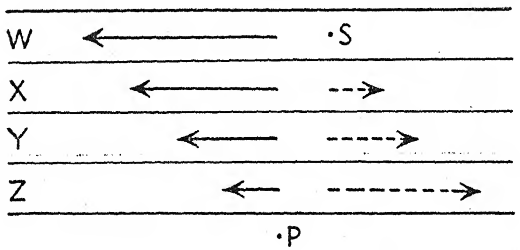


FIG. 5.
For explanation see Text.

see presently that it does represent a reality over a large stretch of the Southern Ocean. In the open sea the effect of wind is to propel and *deflect* the different water layers down to some 150 metres, according to the strength of the wind, through a series of different angles from the direction of the wind, to the right in the northern hemisphere and to the left in the southern hemisphere [4]. But apart from these frequent and various effects of wind we are continually finding water layers flowing in divergent directions as water masses of different density meet, overflow one another, and curve to right or left, or as different layers are affected differently on encountering submarine banks.[1]

We have seen abundantly that the animals vary the extent of their vertical migration. Let us now consider the effect of these changes in behaviour when we have water travelling at different speeds at different levels but, for simplicity, in the same direction. Nearly always the upper layers are travelling

[1] A detailed comparison of the water movements at the surface and those at a depth of 150 metres throughout the South Georgia survey will be found on p. 343 et seq. of the *Discovery Report* already referred to.

faster than the lower ones. Viewed from outside the system at *P*, let the water layers *W*, *X*, *Y*, and *Z* in Fig. 5 be moving to the left at speeds corresponding to the lengths of the arrows. Now let us consider their motion in relation to one of the water layers; let us observe from the surface layer at *S*. The lower layers will now move relatively (i.e. be left behind) with increasing speeds to the right, as shown by the broken arrows. Now in Fig. 6 let an animal in the region *A* be migrating between the layers *W* and *X*. If it is at *a* at midnight on one night it will be at *b*, *c*, and *d* in the surface layer on the next

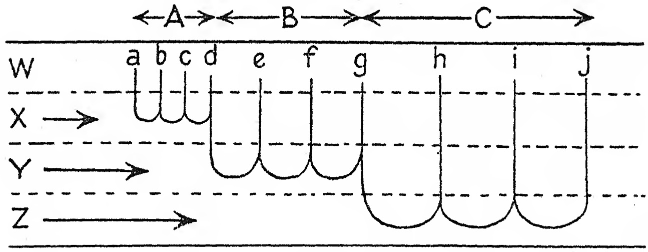


FIG. 6.
For explanation see Text.

three nights. Now if for some reason on coming into the region *B* it migrates more deeply into layer *Y*, it will be at positions *e* and *f* and *g* on the next three nights; similarly if it migrates still deeper in the region *C* it will be at positions *h*, *i*, and *j* on the next three nights following. Exactly the same thing would happen if, instead of migrating more deeply, it went always to the same depth but remained down in the lower layers for a longer and longer time. Now let us consider different individuals of the same species. On the *same night* let there be four individuals at the positions *a*, *b*, *c*, and *d* in the zone *A*; if they each change their behaviour as before on coming into zone *B*, after three nights these same individuals will be at positions *d*, *e*, *f*, and *g*. They will be *farther apart in space*. Likewise in zone *C*, after three more nights they will be at positions *g*, *h*, *i*, and *j*. For a given unit area of surface there will be fewer individuals in zone *B* than in zone *A* and still fewer in zone *C*. If the animals remain higher in the water in regions of poor plant plankton and go deeper, or stay down longer, in regions of rich plant plankton, then this simple dynamical action of the

differing water masses will produce just the effect of diminished numbers in the richer plant plankton zones we have observed. It is quite clear that alterations in the vertical migrational behaviour of the animals, *through whatever different causes*, will bring about alterations in their distribution in relation to their environment.

This applies not only to the physical environment. The animals will continually be brought into fresh communities of organisms. Members of different species, which are close together on one night, will, if they have different ranges of vertical migration, be widely separated from each other on the next night. As the density of the population of most species is by no means constant, even over quite small areas of sea, this process of vertical migration is continually bringing about a reshuffling of the proportions of different organisms in the environment of any one animal.

The plankton animal which has the power of vertical migration is not simply drifting at the mercy of one particular environment, but has a choice. If one set of circumstances is uncongenial, it can descend or rise to another which may be more to its liking. The expert balloonist is not simply drifting helplessly in one particular wind; by the judicious release of ballast or gas he can go up or down until he finds out which stratum of the atmosphere suits his purpose the best. While he cannot go in any direction he pleases, he usually has a choice of several different courses open to him depending on his height of travel. Although he must drift horizontally, he makes use of vertical migration as a means of navigation. The plankton animal can have no sense of navigational direction, but it has the means of selecting the more congenial strata.

Apart from *diurnal* vertical migration, plankton animals may take up *seasonal* changes of level which do actually produce what amounts to an unconscious 'navigation' on a grand scale. In the antarctic there are three main water movements going on in a vertical plane. Against the ice the water is cooled; some of this becomes denser and sinks, but some of it becomes lighter because it becomes less saline with the addition of fresh water from the ice. There is thus a cold surface layer and a cold bottom layer, each continually streaming northwards

away from the pole; in between them is sandwiched a warmer current flowing in the *opposite direction*, flowing south to take their place and be itself cooled against the ice to continue the circulation. The animals in the upper water mass are thus continually being carried away from the antarctic and would presumably perish in time in the warmer lower latitudes. This cold surface current eventually dips below the warmer sub-antarctic surface water, but it continues its way north and its presence is felt even to the north of the equator. In our first South Georgia survey we had an indication that some animals on reaching the edge of the Antarctic Zone sank into much deeper water than usual and so might return southwards with the warmer intermediate layer. Mackintosh [12] in a later survey has found abundant evidence that this is so. In the summer he found the animals higher in the water and so carried away from the pole; in the winter he found them much deeper, in the warmer layer, being carried back. Now, as he points out, this does not apply to all the animals; some, such as *Euphausia frigida* and *E. triacantha*, are making, as we have seen, such a deep vertical migration that they are spending the night in the water going north and the day in the water going south and so maintaining approximately the same latitude. Here is a beautiful example in nature of the conditions we have illustrated in Fig. 4.

Varying degrees of vertical migration are evolved independently in different groups of plankton animals; and species of the same genus may have a markedly different range of migrational behaviour. Animals of different Phyla may have almost parallel behaviours; we were able to demonstrate an association between the amphipod *Vibilia antarctica* and the pelagic tunicate *Salpa fusiformis*; both have a very similar vertical migration.

However vertical migration arose in the first instance, when once established, it has evolutionary significance; it has resulted in providing the animal, otherwise drifting in one environment, with a range of choice.

This essay is intended as a contribution from the sea to the thesis put forward by Mr. Elton from his studies of land ecology. I will end by quoting again from the same work of his with which I started.

'. . . The existence of two sexes, as was shown by Mendel's second law of inheritance, enables hybridization to exploit variations to the fullest possible extent by producing all the possible combinations of mutations already existing in the species. As a result of sex, more material is available in the shape of variation in the characters of animals, and so adaptation is rendered more feasible, or at any rate evolution can proceed faster.

'The migratory impulse, in relation to awareness of environmental harmony, has precisely the same effect in increasing the range of environments with which the hereditary variations can be brought into contact, with a consequent increase in adaptive radiation.'

Vertical migration in the drifting plankton is the counterpart of terrestrial locomotion, it leads to the continual presentation of new environments. By dropping or climbing out of these, the animal itself has some, if limited, power of selection. A new variation which might be doomed to failure in a fixed environment may have the chance of survival in a changing one. With the continual variation in the speed and direction of different water layers, a vertical oscillation provides a small drifting animal with powers of migration corresponding to extensive horizontal movements on the land; a rise and a fall of a hundred feet may mean a horizontal displacement of more than a thousand. This must primarily be concerned with *change*; it is not movement to a particular habitat; each migration brings it into a fresh environment, always unknown to it. The widespread occurrence of this behaviour in the pelagic world, in so many different groups of animals, must be some measure of its importance in the evolutionary process. Any attempt at a discussion of the philosophical implications of this deep-seated capacity for choice in the animal kingdom between what is good or evil for the species (and perhaps the race) must lie outside the confined limits of this essay.

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THE EVOLUTION OF BREEDING SEASONS

By JOHN R. BAKER

FEW subjects call more urgently for an evolutionary and ecological outlook than that of breeding seasons. The great intrinsic interest of physiological research on means whereby reproduction may be started and stopped in the laboratory may obscure the very nature of the problem that is being investigated. This may be illustrated by a simile. If an intelligent savage were given a model steam railway engine, he might make many interesting observations on its functions. He might study its locomotion on sand and under water and discover ways in which its progression could be started and arrested. He might find the effectiveness of mud, clubs, &c., as arresting agents. Yet his studies would lack something if he did not know that the ordinary ecological behaviour of an engine is to run in air on rails, and that its progression is designed to be controlled by the throttle and brake. The design of the throttle and brake is an example in the simile of the directive agencies in evolution, whatever they may have been.

The absence of the evolutionary outlook has been a factor in the slowness of the growth of knowledge about the causes of breeding seasons, but another potent cause has been the inexactitude of much of the observational work. If rapid progress is to be made with the scientific study of periodicity in reproduction, the lax terminology in present use must be supplanted by a more definite one. One reads that the breeding season of one bird is this, the nesting season of another is that. Does nesting mean building a nest, or does it include laying eggs in it and sitting on them? The best information is the egg-laying season in the case of birds, together with the length of incubation, and the copulating season and duration of pregnancy in the case of mammals. In the absence of direct observations of egg-laying, hatching, copulation, or birth, much valuable information could be obtained if field workers would record the egg-season and the pregnancy-season, i.e. the

seasons when living eggs (fresh or incubated) or pregnant females are found.

Animals have evolved the capacity to respond to certain stimuli by breeding. In cold and temperate climates it is usually clear that the season adopted allows the young to grow up in favourable climatic conditions, and one may say that in a sense these conditions are the ultimate cause of the breeding season being at that particular time. There is, of course, no reason to suppose that the particular environmental conditions favourable to the young are necessarily the one or ones which constitute the proximate cause and stimulate the parents to reproduce. Thus abundance of insect food for the young might be the ultimate, and length of day the proximate cause of a breeding season. Agencies which start and stop reproduction but which do not operate under natural conditions of existence may be called artificial causes.

In the wet tropics it is very hard to assign any ultimate cause for a breeding season, for there is no regularly recurring period of food-shortage or cold. If, however, animals were to breed all the year round, there might be great over-population, with disastrous results in any exceptional food-shortage. It is often assumed that all animals are everywhere breeding as fast as they can, but these words are meaningless and it would be equally sensible to say that they are breeding as slowly as they can. Many tropical birds only lay two eggs in a clutch, though they belong to genera in which five or six eggs are the rule among temperate representatives [47]. With some birds, such as the kite, *Lophoictinia isura*, and other Australian hawks and also the cockatoo, *Calyptorhynchus funereus*, it is the regular rule for one of the young to die in the nest [13].

It is true that in parts of the wet tropics some birds are said to have breeding seasons extending all round the year. This applies, for instance, to certain birds of South Kamerun [14] and New Britain [42]. Examination of the data shows, however, that in only a few species are there good reasons for supposing that reproduction is really non-seasonal. Some authors have shown a disposition to follow the example of a well-known ornithologist, who has published these words on the African duck, *Anas sparsa*: 'It undoubtedly breeds throughout the year in the tropical regions, though there are

no data to corroborate this statement.' Occasional species may breed all the year round in certain places (e.g. the fantail-warbler, *Cisticola cherina*, in Madagascar [55]), but the general rule throughout the tropics is for birds to have breeding seasons. The Oxford University Expedition to the New Hebrides, which went to the wet tropics particularly to study this question, was struck by the seasonal behaviour of organisms in a little-varying climate. The climax was presented by the insectivorous bat, *Miniopterus australis*, the adult females of which all become pregnant once a year about the beginning of September, despite the constancy of climate and the fact that they hang all day in a dark and almost thermostatic cave [9].

In temperate climates breeding seasons are usually annual. Periodicity involving longer times is a necessity in those few mammals whose pregnancy extends over more than twelve months, but it appears to occur also in other animals for less obvious reasons. Thus, for example, curlews and other northern-breeding birds sometimes remain throughout the year on the African coasts without reproducing [12]. A large proportion of the big African vultures are accustomed to skip a breeding season [35]. It is not rare for Arctic birds to do the same. Much more common is the existence of two breeding seasons in the year in many tropical birds. This was known a long time ago to apply to many of the small and middle-sized birds of Brazil and Guiana [27], and it is now known to be a widespread phenomenon in the tropics [6].

The effect of latitude on breeding seasons is usually simple in the boreal and temperate zones: the nearer the pole, the later. Thus, for instance, barnacle *nauplii* appear in the seas of west Scotland some weeks later than off southern England, and red deer commonly cast their antlers in April in England and May in Scotland. This rule applies to most birds. The lateness of breeding by birds in the Arctic may in many cases be ascribed rather to their late arrival than to the environmental conditions in the breeding-place. In the subtropical zone the breeding season is sometimes longer than farther north, starting earlier and ending later.

It is interesting to follow breeding seasons right across the tropics to the southern hemisphere. This has been done in detail for the widely distributed old-world birds [6]. No single

rule of general application can be laid down, but certain tendencies can be illustrated diagrammatically.

The breeding seasons of eight species of Fulicariae (moorhen, coot, &c.), chosen for their wide distribution in latitude, are shown in Fig. 1. The striped areas represent the extent of the egg-season. The densely striped area is the usual season and the lightly striped area is the exceptional season of some species or the usual season of a few. Passing south from the northern temperate zone, one finds the egg-season rather longer in the subtropical, but it begins at about the same time. In the northern tropical and equatorial zones it is definitely later, but a second season in the year has sprung up. This is apparently simply the southern hemisphere egg-season, which here again is later in the equatorial and tropical zones than in the subtropical. It is unfortunate that data are not available to bring the diagram into the southern temperate zone.

The sixteen species of widely distributed Accipitres (hawks, vultures, &c.), whose egg-seasons are shown in Fig. 2, present an interesting difference from the Fulicariae. The egg-season becomes progressively earlier as one passes from the boreal to the northern temperate, from the latter to the northern subtropical, and from that to the northern tropical and equatorial, so that in the hot regions of the northern hemisphere the season is mainly from December to March. Here again a second season manifests itself in the equatorial zone, and this second season is seen to belong to the southern hemisphere. In the latter, as in the northern, there is a tendency for the season to be earlier in the tropics than in the subtropics. The Accipitres seldom have two separate breeding seasons in the year, and in the equatorial zones different species adhere to either the northern or the southern season. This is a difference from the Fulicariae, in which group the same species, and probably the same individuals, adhere to the régimes of both hemispheres near the equator.

These examples illustrate two of the characteristic ways in which the egg-seasons of birds cross from hemisphere to hemisphere [6].

Some birds seem almost insensitive to latitude. Thus the Indian hornbill, *Dichoceros bicornis*, starts breeding in January—February in the subtropical, tropical, and equatorial regions.

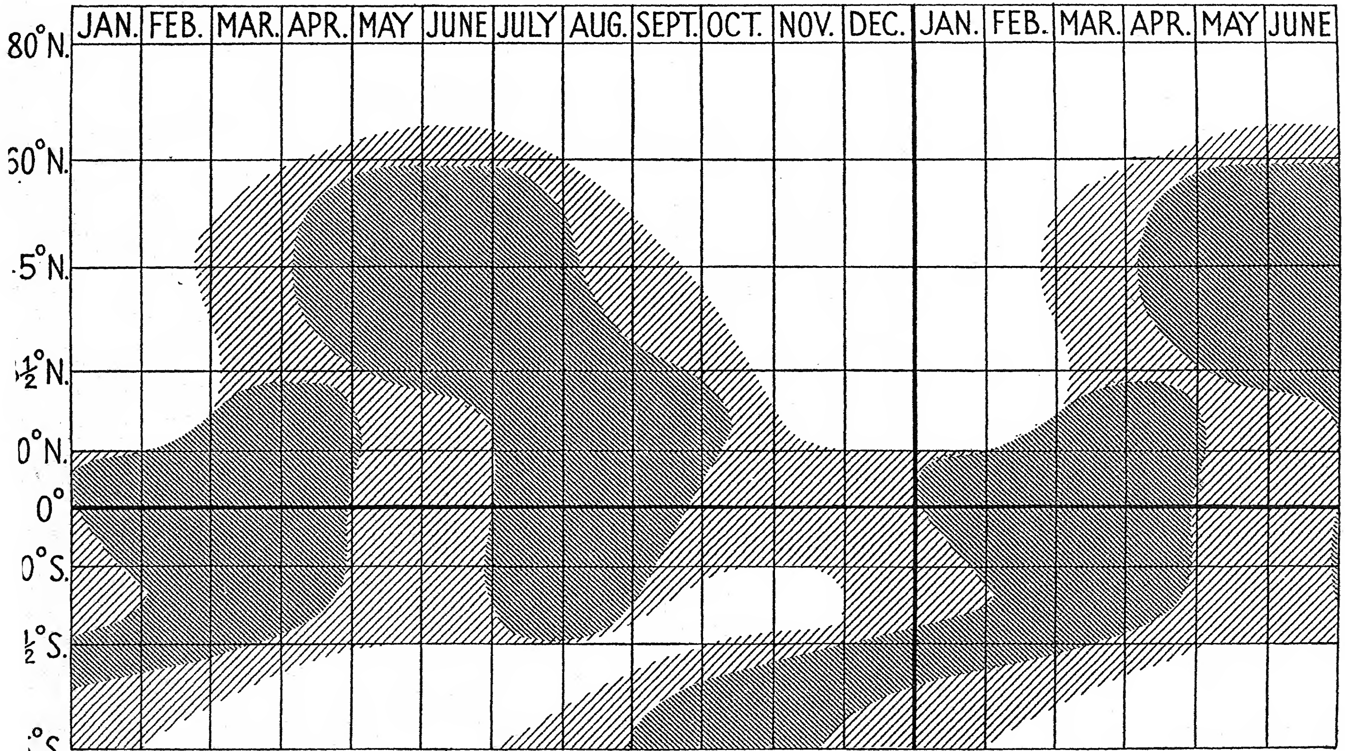

FIG. 1. The egg-seasons of eight widely distributed Fulicariae.

More remarkable is the secretary bird, *Sagittarius serpentarius*, which starts breeding in July—August both north of the equator in the Sudan and south of it in tropical and subtropical South Africa. The albatross, *Diomedea immutabilis*, which departs so far from the habits of most of its relatives as to breed north of the equator in Hawaii, starts laying eggs in the notodune (southern spring), as though it remembered its southern hemisphere ancestry.

The proximate causes of breeding seasons are of two quite different kinds. First, there are such external factors as temperature, light, and rainfall. The organism may be supposed to have evolved until it attained the capacity to respond to one or more factors of this kind by breeding. There is also an internal rhythm in reproduction, which may be so strong as to cause specimens of southern hemisphere birds, imported into the northern hemisphere, to continue breeding at the same time as the others of their species in the south [11]. Internal rhythm can never account wholly for the timing of breeding seasons, for it would get out of step with the sun in the course of the ages [7], but it is likely that it plays its part in making many species quick to respond to the external factors. Probably it is internal rhythm that causes the ferret to begin its spermatogenesis in December [1], even though the start of actual reproduction can be controlled externally. Conversely, it is likely that internal rhythm prevents the swallow from breeding in South Africa in the southern summer, despite the general suitability of the environment. Internal rhythm probably also prompts all members of a migratory species to leave their non-breeding quarters at about the same time, although the environmental conditions may vary widely in different parts of the range. If a migratory bird in the tropics or subtropics fails to migrate to its boreal or temperate breeding-place when the proper time comes, it sometimes nevertheless assumes its breeding plumage [62], although the environmental conditions are so very different from those in which that plumage is usually assumed.

Age is sometimes an internal proximate cause affecting breeding seasons. Thus in Algeria young specimens of the hemipode, *Turnix sylvatica*, lay eggs of both broods a month later than adults [25].

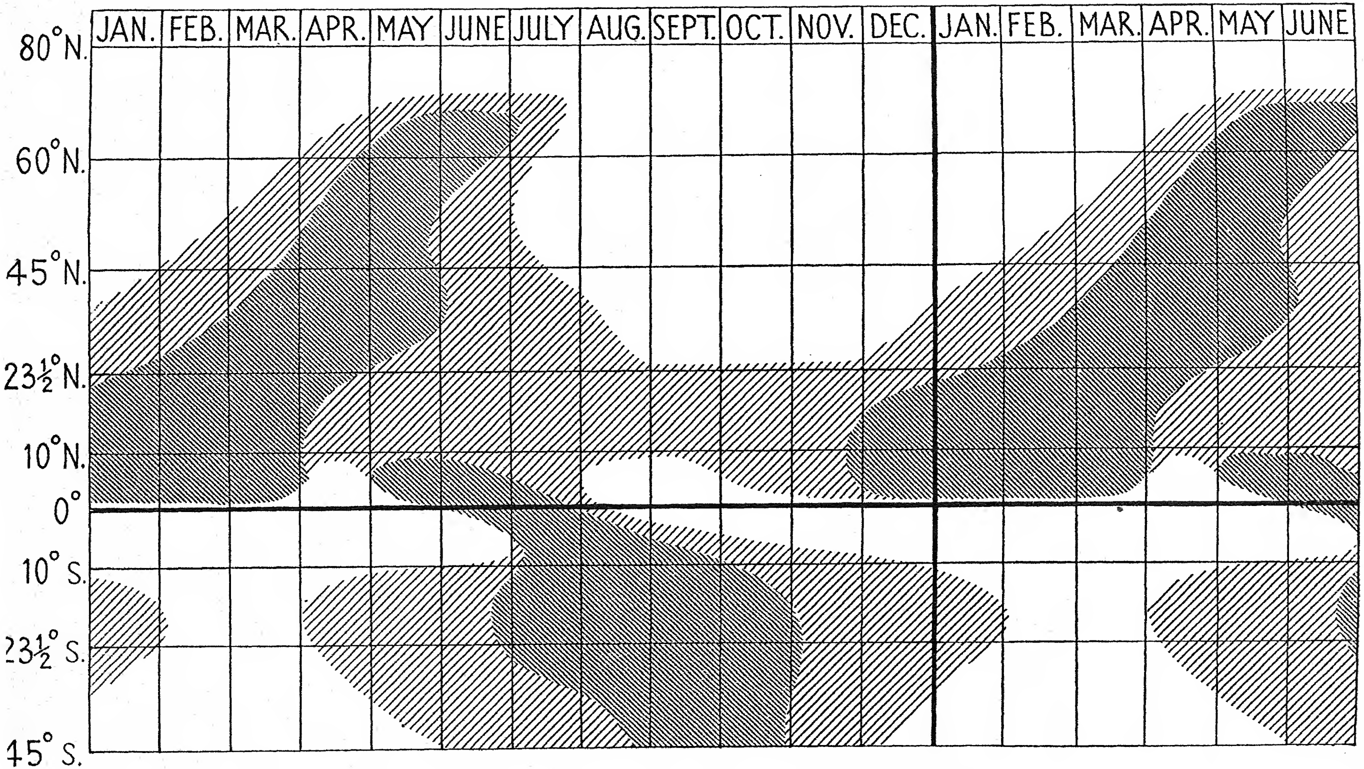

FIG. 2. The egg-seasons of sixteen widely distributed Accipitres.

Of external proximate causes, attention is mostly focused to-day upon light. It has long been known that light influences egg-production in fowls. The discovery that it can control reproduction by male birds [58] and by mammals [10, 17] has opened up a large field of physiological research of the utmost interest [2, 30, 39, &c.; see especially 38]. It is probable that light plays an important part in the control of breeding seasons in some of the animals of the temperate zone. Stress has chiefly been laid upon length of day. It should be recollected that before the spring equinox the days are longer the farther one goes south, while after that date they are longer the farther one goes north: thus, if length of day is really the important factor, there should be a reversal in the effect of latitude according to whether the breeding season starts before or after the equinox. It has been shown [39] that intensity of illumination is as important as duration, and the significance of this for the tropics has been pointed out [4]. Some species of birds have quite different breeding seasons on the two sides of Ceylon, and it is thus certain that length of day does not control them. It is possible that intensity of visible or ultra-violet illumination is the cause.

Length of day may achieve its results partly by giving more opportunity for exercise [59], but *reductio ad absurdum* proves that other factors than this must be concerned with equatorial birds. From about 22 December to 21 June the days are getting longer everywhere north of the equator: in the other half of the year they are getting longer throughout the southern hemisphere. It has already been stressed that equatorial birds mostly have breeding seasons: therefore, if length of day were the only proximate cause, there should be a difference of six months in the breeding time on the two sides of an imaginary line of no thickness! One hesitates to imagine what would happen when a nesting site is actually on the equator, or to conceive what physiological processes would occur in the gonads of those innumerable birds which are continually crossing the equator in their daily search for food. It is easy to try to get over the paradox by believing comfortably in vague breeding seasons or none at all in the tropics; but actually birds generally stick to breeding seasons even when the equator transects their nesting site [51, 52, 53]. In the case

of the domestic fowl, which everywhere breeds all the year round, there is far more seasonal variation in egg-production within the tropics [66] than one could expect if length of day were the controlling factor.

It is the increase, not decrease, in duration or intensity of illumination that is known to stimulate reproduction, and thus organisms which start to reproduce when the days are shortening present a special problem. Ruminants are a well-known example, and the fruit-bats also almost everywhere copulate in the heterodune ('autumn') [5, 8]. As examples of heterodune breeders among birds in the tropics one may quote the sand-martin, *Riparia paludicola*, wood-hoopoes (Phoeniculidae), the small bustards and the ostrich in the Sudan [36], and many of the water-birds of Southern Rhodesia [54]. In Britain the woodpecker, *Dryobates minor*, sometimes starts making its hole in a tree-trunk as early as mid-November [25], while the remarkable parrot, *Nestor notabilis*, breeds in mid-winter in the Nelson Province of New Zealand, despite the severe weather [43].

If one looks to light as the controller of reproduction in heterodune breeders, one is inclined to postulate that the response is to diminution in its duration or intensity; but it may be suggested that this is not necessarily so. It is possible that they are giving a delayed response to the increase of light earlier in the year. This is rendered probable by the fact that in roe deer (*Capreolus caprea*) the period of rut [34] comes so soon after the longest day that it seems incredible that they should be sensitive to the change; while it is equally unlikely that this species should differ fundamentally from other deer in response to light. It would be interesting to find whether one could cause sheep to breed earlier by giving them a larger light-ration in the spring or summer. One might thus accelerate the action of the internal rhythm causing them to breed some time *after* a period of increased light.

It has long been known that there is a connexion between the phases of the moon and breeding seasons in certain marine invertebrates. The pearl oyster on the Great Barrier Reef breeds in May and again in November, on both occasions at the time of full moon [61]. The coral, *Pocillopora bulbosa*, on the contrary, would appear to choose the full moon at one and

the new moon at the other of its two breeding seasons in the year [40]. Conjugation takes place chiefly on the day following the new moon in the ciliate, *Conchophthirius*, in India. The suspected relation between the moon and menstruation in women has, however, been disproved on careful statistical investigation [26].

Temperature is an environmental proximate cause which has been greatly neglected by laboratory workers, although practical men have long used it to control reproduction in freshwater fishes in aquaria. Its importance for marine invertebrates has been demonstrated [48]. General geniality of climate has been stated to make for earlier breeding in birds. Thus the lark (*Alauda arvensis*), which usually starts breeding in the middle of April in Germany, begins at the end of March in very good weather [45]. Similarly, the time varies in the moorhen (*Gallinula chloropus*) from mid-April to mid-May, according to the mildness or severity of the season [25]. The egg-laying of the fieldfare, *Turdus pilaris*, and other birds [33] and of the frog [60] is arrested by a sudden cold snap. The domestic hen lays fewer eggs if the temperature is lowered to near to freezing-point or raised above 23° C. [28]. Wind has been suggested as a deterrent to breeding in equatorial birds [42]. The pH of the soil controls the duration of the reproductive phase in a Collembolan [37].

Food probably plays a part as a proximate cause of breeding seasons in some organisms. Even in equatorial rain-forests, where the physical environment is so constant, most of the fruits are produced seasonally, and this may affect many kinds of animals. If the field-mouse, *Microtus agrestis*, be fed wholly on its usual foodstuff, grass, one can control its reproduction in the laboratory by means of an electric light switch [10]; if, however, it be fed on the optimum food for rapid reproduction, one cannot stop its breeding by darkness. Conversely, starlings will not respond fully to light if kept on a poor diet [18]. These observations indicate that breeding seasons are probably often controlled by the interaction of two or more separate proximate causes. One may prevent rats from ovulating by restricting the protein in their food to casein, and start it again by adding gliadin [49], but this is presumably an example of an artificial cause of reproductive periodicity.

Rain is a factor in the control of breeding seasons whose importance is well known to many naturalists, especially in tropical and subtropical countries, but which has been overlooked in physiological experimentation. Prolonged drought may completely prevent breeding. In a period of drought in western Queensland, no evidence was seen of any bird breeding during nearly seventeen months [23]. Drought in south-east Oklahoma one year resulted in no eggs of lizards or snakes being found in the usual months (June, July and August) [63]. In very dry weather the painted 'snipe', *Rostratula benghalensis*, ceases to breed [3]. The cockatoo, *Kakatoe roseicapilla*, defers breeding till it rains, and may perhaps skip a season altogether if it is dry [41]. The so-called 'fire-quenching' rains (September to early October) of Nyasaland are a great stimulus to the breeding of many species of birds, and it seems that if the rains fail, they do not nest at all (15). The tendency of tropical African birds to breed whenever the rains start has been remarked by several naturalists [e.g., 29], and it has been pointed out that those species which breed in the spring in the subtropical parts do so in the tropical regions whenever the rainy season happens to be [21]. Many species of Australian and Indian ducks start to breed when the rains start [24, 50]. In India the breeding season of the rail, *Hypotaenidia striata*, depends on the time of the rainy season [3], and this becomes particularly striking in Ceylon [65], where the south-west monsoon, affecting one side of the island, comes at quite a different part of the year from the north-east monsoon, affecting another part. The egret, *Egretta intermedia*, lays its first eggs in India within a fortnight of the first good downpour of the rainy season, the time of which varies in different years [3]. Similarly, the salamander, *Amblystoma maculatum*, comes to the breeding pools in Michigan, U.S.A., on the first rainy night after the thawing of the ground, and starts breeding at once [19]. The toad, *Scaphiopus bombifrons*, breeds in North America at the first heavy rain after the middle of spring, and if the rain is late the egg-laying season may be delayed until the end of summer [64].

Aquatic animals are by no means the only ones whose breeding is affected by rainfall. The lizards and snakes mentioned above illustrate this. Many passerine birds are affected.

The mynah, *Acridotheres tristis*, is thought to breed earlier in Assam than in other parts of subtropical India because the rains are earlier there. The oriole, *Oriolus xanthornus*, breeds later in Ceylon if the rains are delayed. The same applies to the fantail-warbler, *Cisticola juncidis*, in Burma [3]. The breeding season of the wood-swallow, *Artamus melanops*, in western Australia is stated to depend on rain. It breeds either in February—March or in June—July or in both seasons, according to whether it rains [57].

The receptor whose stimulation causes certain animals to breed when it rains is unknown, nor is it clear whether the stimulant is the rain itself or the small saturation deficit of the atmosphere or the existence of ponds or floods. It has been suggested that in the Cape Verde Islands it is the green vegetation resulting from the rain, rather than the rain itself, which causes most birds there to breed in the heterodune ('autumn') [20]; and actual drought may act by reducing the food-supply [23].

Although it seems impossible to escape the fact that in some species rainfall is a stimulant to breeding, yet there are examples of animals whose breeding season falls largely within the rainy season without the rain being the determining cause. It is stated that in north Tanganyika the birds' gonads probably begin to grow just *before* the 'short rains' of November—December [44]. Similarly, on the east coast of Madagascar, the general breeding season of the birds starts *before* the rains, though in the island as a whole there is a general correlation between breeding and the rainy season [55]. It has been stated [47] that in those parts of the tropics where the seasons are sharply demarcated by differences in rainfall, most birds breed towards the end of the wet season, while in the constantly wet equatorial regions the tendency is for breeding to occur in the least wet part of the year. It is doubtful, however, whether this rule has any general application.

Rainfall affects the breeding seasons of some birds in an indirect way. The kingfisher, *Ceryle rudis*, makes tunnels in the river-banks both in Egypt [21] and in India [3] when the water has fallen far enough for it to do so. Exactly the same thing is recorded of the sand-martin, *Riparia riparia*, in India, and it is even said [3] that in the same country the kingfisher, *Halcyon*

smyrnensis, breeds two months later in the canals than in rivers, because in canal banks there is no danger of flooding! It is difficult in such cases to disentangle ultimate from proximate causes. In Bear Island (Barents Sea) the tern, *Sterna macrura*, lays about three weeks later on land that is water-logged during the earlier part of the season than on dry ground [33].

An especially interesting case in which breeding appears to be determined by the availability of somewhere to breed is afforded by the Indian koel, *Eudynamis scolopaceus*, which in Bengal lays in December—January in the nests of the early breeding jungle-crow, *Corvus coronoides*, and in May—June in those of the house-crow, *Corvus splendens* [3]. Many observations have been made showing that egg-laying is often dependent on much more subtle environmental conditions than light, temperature, &c. This is particularly well known to aviculturalists. A change in the kind of nesting-box or the presence of an unfamiliar bird may completely prevent egg-laying at the proper time [33]. The higher centres of the brain are clearly concerned in such cases, and it would be almost as futile to look solely to light as the controlling cause as it would be to play with the idea that it is magnetism that draws people into the dining-room about one o'clock. Probably mammals are in general less sensitive to subtleties of this kind than birds, partly because it seems to be the act of egg-laying that is chiefly concerned. The requirement that the environment should be just right in subtle ways, difficult to express in terms of physical science, probably plays an important part in preventing many apparently healthy animals from breeding in captivity, but it is difficult to assess the significance of this factor under natural conditions. In some species under certain circumstances it is probably the final proximate cause; but however right the subtle environment may be, there will be no breeding if the more obvious proximate causes have not ensured that the animal is in a condition in which reproduction is possible.

Human beings are probably less sensitive to subtle proximate environmental causes and certainly less sensitive to the more obvious ones than most higher animals, so that they reproduce all the year round in hovel and palace alike. Most monkeys also have no definite non-breeding season [67]. Many people

are subjectively aware of an increase in sexual urge in spring. In Japan, Korea, and Kwantung, births are particularly frequent in winter, which may perhaps be correlated with more copulations in spring. To the north, in northern Manchuria, the time of most numerous births is delayed to spring, and to the south, in Formosa, it occurs in spring and summer [46]. These generalizations apply both to the Japanese and to the native inhabitants of the places mentioned. It is not very unlikely that the people of the far-distant future will plan an annual breeding season, and that there will be an annual crop of babies at the time of the year most appropriate for their welfare. This should be when the doctors are least likely to be engaged in combating epidemics. It is stated [31] that babies born in March in North America tend to live longer than those born in other months. If it could be arranged that the sexual urge were quiescent outside the copulating season, some of the problems of life would be simpler and more time would be available for important things that is now devoted to trivial ones; but whether hormone therapy makes that possible or not, modern methods of contraception would already make a baby season easy to achieve.

During geological history there have no doubt been variations in the intensity of seasonal change, to which animals must have adapted themselves by changing their response to proximate causes. If one supposes that glacial periods were caused by the earth's orbit becoming unusually elliptical, with resulting coldness in whichever hemisphere passed its winters in aphelion, one must imagine that the animals became adapted to greater seasonal change in temperature but not in length of day. If sunspots were the cause, from the resultant storminess upsetting the even streaming of water away from the tropics towards the poles, the seasons were again probably more sharply defined by temperature changes in the cold periods than in the intervening warm ones [32], but length of day would, of course, everywhere have been the same as now. If glaciation were caused by the large extent and high elevation of land in the polar regions [22], there are no strong reasons for supposing much difference in the amount of seasonal change; but however glaciation is accounted for, the animals were pushed south by it and must have found themselves in regions

where there was a lessened seasonal change in length of day. It is only if there were a change in the tilt of the axis of the earth in relation to the ecliptic that the seasonal change in length of day would become greater or less. If this were to happen, the seasonal change in temperature would vary with that of length of day. It is customary to frown upon the concept of change of tilt, but the possibility of its occurrence appears to merit further investigation [32].

The causes of breeding seasons will never be understood without study of the natural environments in response to which they have evolved, and this is one reason among many why it is to be hoped that natural vegetation will be allowed permanently to cover parts of the earth's surface as a heritage for future generations, and why the capricious setting free of exotic organisms will be branded as the vandalism that it is.

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THE EVOLUTION OF THE NERVOUS SYSTEM AND OF THE RELATIONSHIP OF ORGANISM AND ENVIRONMENT

By J. Z. YOUNG

KNOWLEDGE about the course of the evolutionary history of animals and plants, being based largely on the fossil record, has necessarily dealt mainly with changes in visible form. In studying the nervous system, however, our attention is attracted not to the shape of the constituents but to the part which they play in the self-maintaining activities of the organism. Investigation of the evolution of the nervous system is therefore especially valuable to the general biologist because it serves to emphasize the changes which have taken place during evolutionary history in the relationship between organism and environment.

It will not here be suggested that an evolutionary scheme of classification by itself provides a satisfactory basis for the study of behaviour mechanisms. The time when the study of phylogenetic histories was the primary aim of biology has already passed by. All reasonable persons have now been convinced that evolution has occurred; the main Darwinian thesis has been accepted and needs no further proof. In modern biology the study of the past history of life is of importance not so much for its own sake as to assist in the study of organisms as they are to-day. The general biological problem is to arrange our knowledge about organisms in such ways as shall best serve to meet human needs, spiritual as well as bodily. We shall adopt the method of approach which promises to show us those facts about the composition, development, and life of men, plants, and animals which may make it possible the better to control them for the benefit of mankind.

In pursuing this aim neurology, like the rest of the biological sciences, can turn for its central thesis to a concept at least as old and much more familiar than that of evolution, namely, of the organism as a system which maintains itself by doing work, preserving its distinctness from its environment, with

which it stands in unstable equilibrium. This emphasis on the direction of biological activities is curiously unpopular among some biologists, the word 'teleological' being (wrongly) applied to it, as a label of undiscriminating reproach. Yet it is impossible for any one concerned with living things to ignore this point of view. As Henderson [11] puts it, 'living things preserve or tend to preserve an ideal form, while through them flows a steady stream of energy and matter which is ever changing, yet momentarily molded by life; organized in short.' The very object of our study as biologists is this organization and its preservation, it is 'the first *fact* which strikes us about organisms' [24, p. 290], and it is, as Woodger remarks, curious that it should be necessary to draw attention to it.

There is indeed a danger that emphasis on the fact that many of the activities of the organism are directed towards preserving its organization will be taken by those of animistic temperament as involving the postulation of their particular principle, necessarily ordaining that all organic activities shall co-operate to one end. The question of the nature of the organization by virtue of which any system, whether living or non-living, comes to have its peculiar characteristics is indeed a fundamental one, not lightly to be dismissed (see Woodger [24, p. 440]; Needham [17, p. 12]). But the danger of misinterpretation on such wider issues cannot excuse us from emphasizing the presence of a self-maintaining organization in living matter, especially since nearly all of the practical aspects of biology are ultimately concerned either with keeping organisms alive or with killing them.

The thesis is, then, that profitable arrangement of our knowledge about the functioning of the nervous system can be achieved by considering the part which it plays in the complex of processes by which the organization of the living animal is maintained. We must therefore consider briefly the general nature of this organization and of its evolution.

With the possible exception of viruses and resting spores all organisms may be considered as in unstable equilibrium with their environment. Their organization is such that in them energy changes are continually brought about which are so directed as to prevent the dissipation of the organism into its surroundings. It is a striking and characteristic feature of

living organisms that many, though not necessarily all, of their actions contribute to maintaining this balance. For example, when the difference between our own aqueous system and the relatively dry surroundings is reduced by evaporation, then the complex mechanism of thirst comes into play. Afferent nerve-fibres in the throat are thrown into activity, streams of nerve impulses reach the central nervous system, as a result of whose further activities energy obtained by oxidation of the food is transformed into external work by the muscles, water is sought, raised to the lips, and drunk, and the difference between the composition of organism and environment restored.

Of course not all of the differences between organism and environment are thus dynamically maintained. Once the animal has grown, much of the matter within it may be considered as cut off and work is not needed all the time to keep it separate from the environment. But this does not alter the fact that one of the characteristic features by which we recognize a living organism is the presence of these processes which are so adjusted as to keep the organization intact, and even to increase, by growth and reproduction, the amount of matter thus organized.

All studies of living organisms, therefore, resolve themselves largely into an examination of the organization which makes this self-maintenance possible. This is to say that all biology is in essence morphological in that it deals with the organization of matter or of flux of energy.[1] This truism, often ignored, applies of course as much to biochemistry and biophysics, which study the organization of substances and processes within the organism, as to cytology and anatomy, which describe the visible appearances of the parts (see Peters [19]).

It has long been recognized that the organization of living systems is not in all cases equally complex, but that in some sense we can recognize 'higher' and 'lower' organisms. The definition of degrees of complexity of organization is so difficult a matter, however, that many have been led to reject all discussion of the subject as unprofitable. Nevertheless it is an aspect of biology which cannot honestly be avoided, and consideration of it does in fact serve to make plain some most

[1] Whether biology differs in this respect from the physical sciences is an interesting question which cannot now be approached.

important aspects of the relationship of organism and environment.

One sense in which degrees of biological complexity can be clearly distinguished may be shown by an analogy. In order that a man shall carry a given weight for a given distance at or near the top of Mount Everest there is necessary an organization *more complex* than that required for a similar job near sea-level. The man on the mountain requires special clothes, food, ice-axes, oxygen, and many other things which are not needed by the other. We may say that the former environment is a difficult and the latter an easy one for the performance of such work, and that a more complex organization, and probably also a greater expenditure of energy, is necessary to do the work in the one than in the other.

Now some organisms may be said to live in 'more difficult' environments than others. A marine protozoon is an aqueous salty system in an aqueous salty medium, but a man is an aqueous salty system in a medium in which there is but little water and most of that poor in salts. In fact some organisms have acquired during the course of their evolution the capacity to maintain themselves in environments which are inaccessible to others, they can maintain a greater difference between themselves and their surroundings. Life in these 'more difficult' environments requires special tricks which are not needed when the difference between the organism and its surroundings is less. As Sherrington [23] put it in pointing out that this is the sense in which we speak of some organisms as higher than others, 'in the course of evolution a number of organisms have become so adapted to the environment as to dominate it more variously and extensively than do other organisms'. He goes on to point out that this does not involve the unwarranted implication that the 'lower' organism less perfectly fulfils its 'purpose' or 'design' than does the higher. A similar position is often expressed (though, I think, less clearly) by saying that higher animals are more independent of their environment than are lower (see Woodger [24, p. 415]).

Often the amount of energy needed to maintain a given mass of living tissue can be shown to be roughly proportional to the degree of difference between the organism and its environment. As has already been explained, much of this difference is stati-

cally maintained, but in the case of the ionic composition, for instance, we see very clearly how work is constantly being done to maintain the dynamic equilibrium between organism and environment. Thus freshwater crustacea maintain a concentration of salts inside their bodies higher than that outside, by means of a process which involves so much work that they require approximately twice as much oxygen per gramme per hour as do their marine relatives (see Baldwin [3], for further examples). This means that the freshwater form must also find a correspondingly greater amount of food than the marine form, and this may be one of the factors which account for the scarcity of life in fresh waters as compared with the sea.

We can, then, properly and with clear meaning speak of environments as presenting varying degrees of difficulty for the maintenance of living organization. But an attempt at specification of the relative status of any two given types will soon convince us that it is impossible to evaluate the degree of difficulty exactly, though in general the organisms which we refer to as 'higher' maintain themselves in more difficult environments than do the lower. They do so by virtue of their greater number of special mechanisms of adjustment, which give them that greater complexity which we vaguely recognize, and which often necessitate the transformation of greater amounts of energy for the maintenance of a given mass of living substance. In the physicist's terms we may say that some organisms (the higher) are even less probable systems than others (the lower). But organisms similar to each other in many respects maintain themselves each by a special trick under different conditions. In most cases it is not at all easy to estimate which of two environments is the more difficult, nor is it usually profitable to do so.

Of course it cannot be maintained that all lines of evolution proceed by increasing complexity of organization from easier to more difficult environments. In numerous cases the reverse change takes place and we speak of 'degeneration'. Also in every group of animals some become as we say specialized, for life in particular niches, often by such profound modification of their organization that it is very difficult for them to change their environment further.

But the fact which stands out and cannot be ignored is that

during the period since the Cambrian there has been a tendency, widespread but not constant or universal, for some of the organisms to become provided with more complex systems of self-maintenance by redistribution of energy than were possessed by their ancestors. This is especially clear from study of the nervous system. Even though this system can hardly be studied in the fossil state, yet we can say with confidence that in Cambrian times there were no organisms whose neuro-muscular systems approached in complexity those of the modern insects, cephalopods, and vertebrates. The ancestors of these groups then living distributed energy in less manifold ways, they possessed fewer tricks, than do some of their successors to-day; possibly they also distributed quantitatively less energy per unit mass of living substance.

It is probable that there has been an increase during this period since the Cambrian in the amount of matter which is organized into living systems, some of these having become so adjusted as to be able to maintain their organization in situations not previously harbouring life. As the ecologist puts it, they have invaded new niches. But alternatively it is conceivable, though unlikely, that conditions in general have become less favourable for living systems. Perhaps both types of change have proceeded together: environments have altered, and living organisms have colonized new niches.

This discussion of the changing relationship of organism and environment must not be used without careful consideration to support the postulation of any particular driving force in evolution. Theories of the Darwinian type suppose that such evolutionary changes are produced by the operation of those factors which lead to variation and natural selection. But it is often forgotten by biologists that the latter only operates because living organization is such that it tends continually to increase the amount of matter comprised within itself. To say that evolutionary changes are the result of natural selection therefore only restates without solution the general problem of the direction of living activities, a problem which, as has been said (p. 180), needs discussion with extreme care.

But the technical business of the biologist is not to discuss these problems, for which he is not trained. Our primary aim is not now even to make an inquiry into the history of organisms,

however entertaining this may be to ourselves or useful as material for the technical studies of the philosopher. Proper appreciation of the nature of the relationship of organism and environment is, however, important as a basis for our professional business, which is the study and control of living things. In the particular inquiry which we have in hand it is possible to learn much by evolutionary study of the part played by the neuromuscular system and especially by the 'higher nervous centres' in the self-maintenance of the animal organisms in which we are specially interested.

General nature of the activities of the nervous system

The particular characteristic of animal organisms is that not merely do they take substances into their bodies against concentration gradients and thus build up and maintain an improbable organization, but that they actually 'seek out' the situations necessary at any time for the supply of a given material. In a sense they may be said to choose their environment. But we must beware of the use of such terms as 'choice', particularly when, as in this case, they are liable to lead us to leave the matter thus settled with a word, rather than to proceed farther with analysis of the processes by which this choice is produced.

These processes are in fact the activities of the neuromuscular system, whose general role might thus be said to be that of bringing each tissue into contact with an environment suitable for its self-maintenance. The mechanism by which this result is brought about includes so many interacting parts in the more complex animals that any attempt to subdivide and classify its activities leads inevitably to artificial divisions. For grasping the nature of the types of action which the system performs, however, it is convenient to recognize the following parts (cf. Sherrington [23]).

The *effectors*, such as the muscles, cilia, and glands, are the agents by which the animal conveys its body or some part of it into particular environments, and the sum total of the action of the effectors constitutes the *behaviour* of the animal. The effectors produce their effects following the operation of some *driving* or *motivating* forces which control the behaviour at that moment. In each segment or act of behaviour which is effective

in helping towards self-maintenance we can recognize two main sources of motivation. Firstly there are the internal influences by which the activity is made to conform to the needs of the animal at the moment. These forces together make up the *internal drive*[1] or *internal motivation*, and they include such activities as the discharge of nerve impulses by the *internal receptors* or sense organs in the walls of the stomach, bladder, or blood-vessels, which set the activity of the organism in directions appropriate to its needs. Other no less important items of internal motivation are discussed later.

The second type of influence which bears upon each segment of behaviour is that of *external drive* or *external motivation*, including chiefly the nerve impulses discharged by the *external receptors* under the influences of changes in the surrounding world.

This analysis, neither essentially new nor profound, must not be taken too formally. It provides some convenient terms as a frame of reference for description of the immensely complex activities of the nervous system. Such a scheme is particularly useful for study of the evolution of the system because it enables us to trace the changes in the relationship of organism and environment, and directs us in each case to the receptor, central, and effector mechanisms by means of which the organism maintains a great difference between itself and its surroundings.

Evolution of effector mechanisms

The changes of complexity of organization which occur can be well illustrated by study of the evolution of the effector systems. In the case of the muscular system the mechanism for releasing energy as external work by utilization of the contractile properties of myosin has become, along some evolutionary lines, progressively divided into more and more parts. In the historically earlier forms the arrangements of the muscles are mostly such as to produce total movements of the whole animal. The muscular system either acts as a whole or if it is divided into parts these are all similar to each other. Thus the contractions of the bell of a jelly-fish, the wriggling of a polychaete worm, and the swimming of a fish are movements which

[1] The term 'drive' is used in various senses by different writers, being often restricted to what is here called internal drive.

involve either much of the musculature at once or the serial contraction of similar parts. Contrasted with such total movements serving to bring the whole animal into or out of any given environment are the movements of separate parts of the effector system, acting to a large extent independently of each other; each movement serving in some special way in the general labour of bringing the tissues into contact with an appropriate environment. The medusa, worm, and fish already have some such special mechanisms, for instance the musculature around their mouths, by means of which they can to some extent 'handle' their environment. But in the more complex descendants of such forms there is a vastly greater development of special mechanisms. In the arthropods along several separate lines the original series of similar limbs has become modified, providing the animals with a series of tools by means of which they can bring their tissues into conditions which it would be impossible to reach without such equipment. The effectors of the honey-bee may be said to be more complex than those of a polychaete worm because the former can do more things than the latter. Both can walk and eat, and the worm can swim and in some cases secrete a tube, but the bee can fly and collect nectar and pollen and make combs and stock them with honey, clean its limbs, dance to communicate with its fellows, warm or cool its hive, and sting an enemy.

Changes of the same sort can be traced in the evolution of the cephalopod molluscs from an ancestor whose foot served for creeping, to such forms as the modern *Sepia*, which swims actively about with its fins, mantle, and funnel, and can handle the environment in complex manners with its arms. Perhaps the most striking of all of these changes has been the development of the vertebrate musculature, especially among the mammals. The original segmental series of similar muscles, serving to move the animal by their metachronal contraction (see Gray [10], &c.), becomes split up into a great number of separate muscle groups, capable in man of acting almost independently of each other, and yet in a manner so co-ordinated as to serve to provide the materials necessary for life even when these have to be obtained by such devious methods as digging in the earth for coal or writing with a typewriter.

Of course the direction of evolutionary change has not

always been that of development of extra mechanisms in this way, nor is it possible in many cases to compare the complexity of organization of creatures adapted for very different habits. But it is possible to be clear about the sense in which we say that the muscular system of a man is more complex than that of a fish, and it is profitable to draw attention to the difference as indicating the essential respects in which they differ in relationship to their environments.

Evolution of receptor mechanisms

It has often been remarked that all animals are capable of responding to approximately the same general types of change in their surroundings. Nearly all respond in some way to changes in the incident light, heat, and sound waves and to mechanical and chemical changes around them. But in the 'higher' animals the receptors become able to respond not merely to smaller changes in the environment but to aspects of those changes which their ancestors did not distinguish. This can be shown by consideration of the visual systems.

The photoreceptors of animals which have nervous systems consist of cells able to produce their effects by discharging nerve impulses when the intensity of the light incident upon them varies (there are a few exceptions of independent effectors such as the muscles of the iris of vertebrates). It is possible that there has been, during evolutionary history, an increase in the sensitivity of the mechanism of discharge, so that a smaller change in the incident intensity can set off the process which ultimately initiates the nerve impulse. But such increased sensitivity would be useful only in certain habitats and we should expect to find it only in these. It would be ridiculous to maintain that there is in animals a general and universal tendency to increasing photoreceptor sensitivity.

However this may be, the point of interest here is that in the simplest cases change in *intensity* of light serves merely to activate muscle systems, independently of its direction. In other animals the photoreceptors become so arranged that the response depends on the *direction* as well as simply on the intensity of illumination. In others the varying thresholds of the receptive cells to different wavelengths are made use of by the development of a mechanism for response to the different *colours*.

Finally, but only in a very few groups of animals, the arrangement of receptors and of their central connexions is so developed as to make it possible for the organism to respond not merely to the direction but also to the *pattern* of incident illumination, and hence to react differently to different visual shapes. It must be emphasized that these latter capacities are found only in the later groups of animals, and it can hardly be doubted that the great success of the higher vertebrates, and especially of man, in maintaining living organization in unfavourable environments is partly due to the capacity to discriminate between the various patterns of incident illumination, sound, and touch. Though a few mammals manage to find the great amounts of materials which are needed without eyes, yet most make great use of these in the course of their 'improbable' activities.

Evolutionary changes in the receptors, then, have enabled organisms to colonize more difficult environments by making it possible for the organism to react to very small changes going on around it. Ultimately a great variety of aspects of change can be distinguished and this makes it possible for the effectors (suitably modified at the same time) to bring the tissues into relationship with appropriate conditions. Thus the capacity to discriminate colours and simple shapes in the optic system of the bee helps to make possible the use of the special effectors which are present. Similarly in man the development of eye, hand, and brain have gone together.

In addition there must be many special internal receptor mechanisms developed in the more complex animals. Appropriate systems of internal drives are essential for the colonization of 'difficult' environments since the effectors are only suitably brought into play if the internal conditions are driving or setting them appropriately. Unfortunately we have very little information about the internal receptors except in mammals and even in this group we know all too little of their action. The same applies to the other forces of internal motivation such as the endocrine glands (see also p. 200).

Evolution of central nervous mechanisms

It is in the nervous system itself that the change during evolutionary history in the complexity of the mechanism for

redistributing energy appears most clearly. In the simpler animals the nerves serve as *connectors* of the afferent and efferent systems and this function is of course maintained in all later stages of nervous organization. There are certain situations for which one simple act is required, and, to meet these, simple types of afferent, central, and efferent connexions which we call reflex arcs have been evolved. The flexor reflex and blink reflex of man are good examples of reflexes of this sort. In the performance of such acts the nervous system serves essentially only as a connector, the central pathways being in the limiting case inactive except when the appropriate receptor is discharging. But it must be recognized that such a simple situation is very rare and that the nerve-cells which control most muscles are not normally completely at rest but are receiving some nerve impulses even before a sudden afferent volley arrives (see Sherrington [23], Fulton [7], Creed et al. [5]).

There have been special developments during evolutionary history even in the connector function as such. The rate of nervous conduction, for instance, has been increased in some of the types either by increasing the diameter of the nerve-fibres or by increasing the thickness of the myelin sheath, which appears to accelerate conduction in proportion to its thickness. Though clearly comparable data are lacking it seems that for a fibre of diameter 10 μ at 20° C. the rate of conduction is of the order of 1–2 m./sec. in molluscs (cephalopods), 3–5 m./sec. in crustacea, 20 m./sec. in a cold-blooded vertebrate (frog), and 60 m./sec. in a warm-blooded one (at 37° C.) (see Pumphrey and Young [20]).

But increased speed of nervous conduction does not necessarily in itself confer a significant advantage on the organism. We must beware of regarding increase of speed, or of any other single process, as a necessary and constant feature of biological 'advance'. Indeed there is evidence that in some cases animals with slower conduction rates have evolved from those with faster rates in nerves of similar function. For instance, the octopod cephalopods, having developed the use of their arms in walking, have come to use the mantle less than did their decapod ancestors (Robson [22]), and at the same time have lost the large and rapidly conducting axons possessed by the

latter (Young [25]). The time saved by such fibres would presumably not be of significant advantage to the octopus though it can be shown to effect a considerable saving of time for the longer-bodied and more quickly moving squids and cuttlefishes.

Among vertebrates the great speeds of conduction must surely assist in the maintenance of such great masses of living matter as those of man, whale, or elephant in their unpropitious environments. If man had a conduction rate of 1 metre per second, a delay of at least three seconds would be necessary for a response to a touch on the toe if it involved the brain. Such long delays are indeed observed in pathological conditions in which the myelin sheath is destroyed, and they do seriously impair the capacity of the man to obtain the necessities of life.

But the increased biological efficiency of the nervous system of higher animals is not by any means limited to better functioning as a connector of afferents and efferents. The great significance of the large and complicated central nervous systems of the higher forms lies not merely in the fact that they allow certain receptors to activate certain effectors but that they also *allow the impulses from each receptor cell to interact with those from other receptors so as to produce a response different from that following stimulation of the single cells alone.* The basic mechanism providing this capacity is that of summation (or facilitation) of the effects produced by successive impulses in one nerve-fibre, or by impulses in neighbouring fibres.

As Sherrington [23] so clearly pointed out, this interaction is made possible by the fact that a nerve impulse, though it spreads over the whole of any one nerve-cell, does not necessarily pass to neighbouring cells across the synaptic junctions. To produce a spread to other neurons a summation is usually necessary either between the effects of successive nerve impulses arriving along one nerve-fibre at the dendrites of a cell, or between the impulses arriving in the various endings scattered over the dendrites.

We can distinguish two most important types of co-ordination which are thus made possible. Firstly there is that between receptors. A motor path for swallowing may be excited only by the appropriate combination of, say, optic, tactile, and

gustatory impulses (see Herrick [12]). The development of this type of interaction makes possible the integration of the changes which go on at various sensory surfaces so that the animal is enabled to react to a unified 'world' instead of to a series of discrete stimuli.

Secondly, an even more important use of this mechanism of co-ordination is to allow of the co-operation of the various receptors of one sort which are spread out over the surface of the body (see Creed [4]). Thus the impulses from any one receptor cell will differ in the motor effects which they produce according to whether they arrive alone or accompanied by impulses in the neighbouring receptors. This is presumably the basis of the capacity to react to shape or pattern of excitation. Although little progress has been made in analysis of the physiology of pattern discrimination it is probable that some such arrangement as the above provides at least part of the solution for many of the puzzles posed by the 'Gestalt' psychologists (see also p. 198). For the capacity to distinguish shape depends essentially on the presence in a receptor field of mechanisms by which the effect of an excitation shall depend on the ratio in which the various parts of the sensory surface are active. The only physiological mechanism which we can imagine for this is one in which the impulses from the receptors in the various parts of the primary sensory surface converge centrally. Probably the large nerve-centres which are found connected with so many well-developed receptors provide just such a mechanism. For instance, the optic lobes of many arthropods and of cephalopod molluscs provide ample opportunity, by their internal connexions, for interactions between the impulses set up in the primary sensory cells.

The presence of such mechanisms for the interaction of impulses from different receptors also assists in the development of powers of discrimination between a number of qualities within any one sensory field. The definition of 'one sensory field' is perhaps ambiguous in this case; the field of true taste, for instance, may also be considered as composed of four fields, each for a special type of chemoreception. Interaction between the impulses produced by these four types of receptors would therefore be an instance of interaction between the discharge of receptors of different types. In the gustatory field there is in

fact very little such interaction, but in other afferent systems which are capable of discriminating numerous qualities there is probably much interaction between the responses of a few types of receptor. For instance, it is possible that the discrimination between a large number of olfactory stimuli by vertebrates is made possible by the presence of a number of types of receptor (at present unrevealed) in the nasal epithelium, whose responses interact in the olfactory centres of the cerebral hemispheres, which are so surprisingly large even in fishes, in which they receive almost solely olfactory impulses.

The central nervous system, then, by providing opportunities for the interaction of the impulses generated in the various parts of a receptor field makes it possible for the animal to react to various aspects of environmental change which are of great significance to it. In order to be able to fulfil these functions as a co-ordinator the system must provide for abundant interconnexions, so that the functioning of any one part of the receptor system is affected by as much as possible of the rest of that system. For this interconnexion to be possible the nerve-cells are usually grouped into compact masses of tissue, and this is probably one of the factors which have operated to produce the progressive concentration of the C.N.S. which has occurred along so many evolutionary lines. The unconcentrated systems of coelenterates, echinoderms, platyhelmia, and some molluscs probably consist mainly of connecting paths between afferents and efferents, whereas in the great masses of cells in the concentrated nervous systems of cephalopods, arthropods, and vertebrates there are mechanisms for ensuring that the functioning of each part is influenced by that of its neighbours.

The constant activity of the central nervous system

But we have still not exhausted the history of the evolution of the complex capacities of the nervous system. Out of its co-ordinating activities of the above types has arisen another and still more important device for controlling the redistribution of energy in ways conducing to self-preservation. We have so far been considering the central nervous system as if its cells were passive and returned to rest when the receptors

ceased to discharge. Some of the simpler portions of the system may indeed do this, but it is probable that many parts remain in constant activity throughout life. One of the pieces of evidence of the existence of this constant activity is that of the electrical changes which take place in the brain. Electrodes suitably placed on the head of a man, even on the outside of the skull, will record continual rhythmical changes of potential in the underlying brain, the type of rhythm changing under various circumstances such as falling asleep or the performance of mental work (see Adrian [1], &c.). Though these electrical signs of activity are altered by afferent discharges they are not dependent on them. The waves do not cease when all afferent stimulation is cut off. This is strikingly shown by the rhythms which can be recorded from the olfactory bulbs of a frog *even after these have been removed from the head* (Gerard and Young [9]).

The exact nature of the changes in the neurons which correspond to the waves is still unknown. Since the potentials are relatively large they must be due to the simultaneous activity of numerous neurons, but whether this activity is of the nature of the discharge of nerve impulses or of changes of threshold is not known (see Adrian [1], &c.). It is possible that the activity is due to the spontaneous changes in nerve-cells which do not come to rest but go through perpetual cycles of recharge and discharge. Or there may be neurons arranged in chains which perpetually re-excite each other in a circular manner. Ranson and Hinsey [21], and especially Lorente de Nó [15, 16, &c.], and others have shown that there are ample connexions to allow of the establishment of such closed chains of activity in the nervous system, and their possible significance is further discussed below.

Probably similar mechanisms occur in many of the animals which have highly concentrated nervous systems, though they have not been revealed because their significance has not been appreciated.

Significance of constant activity of the central nervous system.

We do not yet know enough about the nature of the self-re-exciting cycles in the central nervous system to be able to say with any certainty what part they play in the life of the animal. Ranson and Hinsey, and Lorente de Nó, have suggested that

they may control reflex after-discharge. But there is reason to suppose that the presence of a continually active system is bound up with the development of the special capacities of adjustment of organism and environment which are characteristic of the most complex animals. It is most difficult to express the nature of these capacities concisely and yet without oversimplification, but some of their main features may be expressed as: 1. The ability to respond to the pattern of changes going on around the body. 2. The possibility of allowing the results of past behavioural patterns to play a part in determining present activities. 3. The development of complex mechanisms of internal drive or motivation, especially such as shall allow the animal to proceed to obtain its requirements by indirect means. The way in which it is suggested that the continuous activities of the central nervous system may help to bring about these forms of behaviour may be illustrated by describing the arrangements in cephalopods.

Possible learning mechanisms in the supraoesophageal centres of Cephalopods.

It is impossible here to discuss the many problems involved in the search for the mechanism of learning. In order to illustrate the possible significance of the establishment of self-re-exciting chains of activity for the process, I shall describe the anatomical arrangement recently revealed in certain centres in *Sepia*.

Some of the cells *A* of the region known as the lobus frontalis superior (*l. fr. sup.*) send axons which make connexions with the cells *B* of the lobus verticalis (*l. vert.*). Some of the axons of these latter cells pass forward again into the lobus frontalis superior and make contact with the neurons *A*. Here, therefore, is a mechanism by which the cells might activate each other in a continuous and circular manner, though it has not yet been possible to determine all the details of the relationship, for instance whether any given neuron *A1* sends impulses to one or many neurons *B*; or whether *B* sends impulses back to the neuron *A1* by which it was excited or to others *A2*, *A3*, &c. We have at present insufficient evidence to show whether the conduction rates and refractory periods are such as to make the cycles possible.

Now other cells *M* in the lobus frontalis superior send axons to various motor centres, and these cells *M* could receive impulses through the dense network of collateral branches from the neurons *A*.

The afferent stimulation of the frontalis superior comes from a very large bundle of optic-tract fibres *O* arising in the optic lobes, in which the primary optic impulses have already had

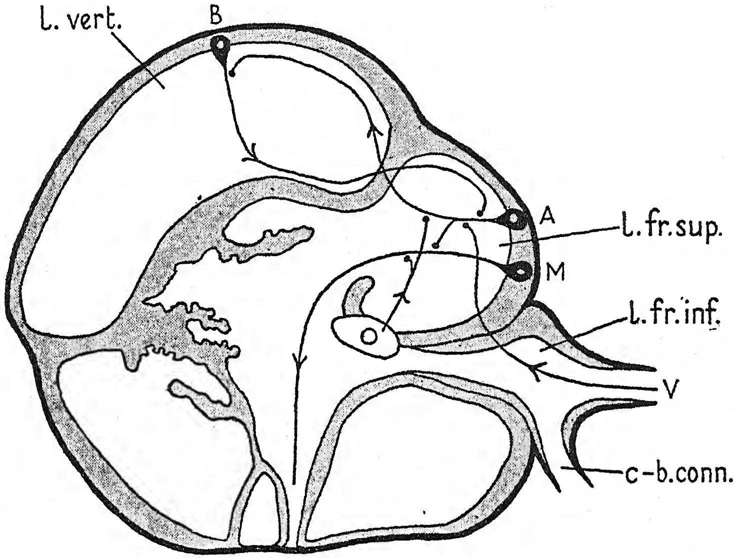

FIG. 1. Diagram of longitudinal vertical section through the supraoesophageal ganglia of the cuttlefish (*Sepia*). Description in the text. The shaded areas represent the nerve-cell layers. The cell bodies are shown disproportionately large.

ample opportunities to interact with each other. Secondly, there is a large tract entering the frontalis superior from the lobus frontalis inferior (*l. fr. inf.*) which is connected with the buccal ganglia, and hence with the visceral afferent fibres *V* coming from the stomatogastric system (see Alexandrowicz [2]). Other afferent impulses may also play upon the cells of both the frontalis superior and the verticalis, for instance tactile fibres from the arms running in the cerebro-brachial connective (*c.-b. conn.*), or chemoreceptor influences from the lobus olfactorius.

It is now worth while to consider how the connexions of these lobes might allow for the formation of a conditioned

reflex involving change in the optic field as the conditioned stimulus and taste or touch as the conditioning stimulus which produces an unconditioned response such as salivation or extrusion of the prehensile tentacles. Suppose that the fibres *M* if appropriately activated produce the state in the lower motor centres which causes the tentacles to be shot out. An inflow of optic impulses does not, in the unconditioned state, excite this response, because impulses at the synapses *OM* alone will not fire the neurons *M*. Nor will impulses at the synapses *OA* fire the self-re-exciting chains which we may represent as *ABA*.

But if the change in the visual field is accompanied by the elicitation of the unconditioned reflex, say by taste or touch, then food will be eaten and visceral afferent impulses will reach the frontalis superior in *V*.[1] These impulses may summate with the optic impulses in *O* to fire off the neurons *A* and hence the chains *ABA*, which thereafter continue their activity.

In the course of each cycle of the chain, impulses reach the synapses *AM*, but these impulses alone are insufficient to fire off *M*. But a subsequent presentation of the visual stimulus will now produce the response, because the impulses in the chain *ABA*, through the collaterals *AM*, summate with the excitation at *OM* to fire off the neurons *M*.

It will be recognized that such anatomical studies cannot do more than demonstrate that connexions are present which might function in the manner suggested. We do not even know that the animals are capable of such conditioning or that the self-re-exciting chains are continually active. But these are matters open to experiment, and in a subject so obscure and important as that of the mechanism of learning it is worth following any clue, and this is the reason for drawing attention to the matter here. The fact that the *anatomical arrangements necessary for such a mechanism are present* is certainly suggestive. It must be remembered that a diagrammatic scheme in which single chains of neurons are shown gives a picture simplified to the point of falsity. Moreover there are types of connexions present which have been omitted, for

[1] Impulses from the receptor which produces the unconditioned response may also reach the frontalis superior. The visceral afferents *V* are dealt with here to emphasize that it is the biologically satisfactory associations which are learnt; but it is impossible now to review fully the question of the conditions necessary for learning.

instance tactile and other afferents firing directly into the lobus verticalis and pathways leaving the latter for the motor centres.

At least this case serves as an example of how the continual activities of the central nervous system *may* play a part in learning. As presented it provides a possible mechanism only for some very simple types of conditioning. The fact that the unconditioned and conditioned stimulus must be presented together or at a short interval of time becomes understandable, as also does the need for reinforcement of conditioning, in the absence of which the cycles of activity might be supposed to get out of step and ultimately to stop.

Another most difficult problem of learning is that 'the response is, within wide limits, independent of the particular sensory cells stimulated' (Lashley [13]). This would be possible with a mechanism such as the above since we can imagine that collaterals from the cycle *ABA* would affect many neurons, *M1*, *M2*, &c., so that they can produce impulses when optic impulses reach them.

It will be noticed that the mechanism postulates the existence in the higher centres of tracts (*M*) controlling each motor activity and the provision of opportunities of connexion of these with appropriate visceral afferents *V* and with such other afferents *O* as may be able to form conditioned reflexes involving *M*. For elaborate patterns of conditioning the neurons of the higher centres would need to be exceedingly numerous, as indeed they are.

This particular scheme does not as it stands deal with the types of learning which are much the most important and difficult to understand, namely those involving discrimination, especially of pattern, and the learning of complex motor patterns. Study of these immediately begins to raise problems of excitation in ratios which cannot be dealt with here (see Lashley [13, 14, &c.]). It is possible, however, to imagine a great variety of modifications of the scheme, including such as will allow only special patterns of optic impulses in *O* so to interact with the chains of activity in *ABA* as to produce motor discharges in *M*.

In general any set of afferent impulses arriving at a centre may be supposed to produce an effect which will depend on the pattern into which it fires. But we know almost nothing

of the nature of these patterns of intrinsic activities in the central nervous system; even electrical studies have not yet told us much about them. But it is not unreasonable to suppose that the patterns of activity within the centres are built up, at least in part, under the influence of the patterns which impinge on them from the receptors. Each afferent situation may be supposed to produce some modification in the cycles.

Of course if the pattern is dynamic it depends not on the particular connexions of neuron with neuron but simply on the order in which they excite one another. The nervous system thus provides a matrix of neurons, interconnected with each other in most varied ways, and the patterns build up and maintain themselves within this matrix. Cessation of the cyclical activity would destroy the pattern since it is dynamic and does not depend on particular connexions. If activity stopped the organism would 'forget' all that it had learnt. Sudden disruption of the patterns in this way might be adduced as the basis of shell-shock and amnesias produced by great fright, &c. More gradual modification might provide the basis of ordinary forgetting.

These are very sweeping speculations which may prove to be only in small part correct. They are emphasized here because it is important to focus attention on the part played by the intrinsic activities of the central nervous system in controlling these more complex forms of behaviour which have so long defied physiological analysis.

The nervous system as a motivator of animal behaviour

It has now been shown that the opportunity offered by the central nervous system for the interaction of various afferent impulses with each other and with a constant background of activity is probably one of the important factors which give the more complex animals their capacity to react to small changes in the world around in such remarkable manners to conserve their own integrity.

The presence of these centres makes the central nervous system the dominating factor in the control of behaviour. In the animals such as the coelenterates and echinoderms in which the nervous system is still diffuse it acts essentially as a connector of afferents with efferents. The self-preservatory character of

the activities of such types of animal depends mainly on the structural pattern of the conduction paths laid down during development. Pantin [18, &c.] has shown, however, that considerable variation in response may be produced even in these types according to the pattern of afferent stimulation, and this capacity develops rapidly with increasing complexity of the nervous system so that students of the behaviour of even such animals as Platyhelmia often stress that they are 'keine Reflextiere'. This should not be taken to mean that the mechanism of their reactions cannot be analysed.

But in the animals in which a large and compact central nervous system has developed, the course of behaviour is controlled not so much by the connexions of afferents with efferents as laid down in hereditary pathways, nor even by the pattern of afferent stimulation, whether external or internal, produced by interaction in such paths. The most important factor in determining the course of a reaction in such an animal as man is probably the intrinsic activity of the nervous system itself, and it is therefore convenient in such cases to speak of the behaviour as controlled by *neural motivation* or a *neural drive*. This is of course a component of the system of internal motivation which also includes the interoceptors and hormonic motivators. Isolation of types of drive in this way is somewhat artificial, but it is convenient for some purposes, and there is a special value in the separate recognition of neural drives since it calls attention to the enormous part played by the C.N.S., a part which should be obvious but which, curiously enough, is often less stressed in this connexion than that of the interoceptors or ductless glands.

To give an example of the use of such terms: the reaction of a hungry man to the presence of food is not always that he eats it. If he has acquired what we call a 'distaste' for it, or if he is on hunger strike, he will refuse it, and in neither of these cases can the main motivation of his behaviour be said to be due to internal or external receptors or to hormones. In so far as we can define it physiologically we can say that it must depend on the activity of the C.N.S., that is to say on neural motivation.

It is true that many, if not all, of the activities of the C.N.S. are ultimately determined by the afferent impulses which

reach it, but it is still convenient, once a pattern of activity has been set up in the C.N.S., to be able to refer to any effects of this pattern in motivating behaviour as a neural drive.

We have more than speculative evidence that central activities do play a profound part in this manner. To give only one example: tumours or lesions of the frontal lobes of the cerebral hemispheres of man or chimpanzees produce 'personality changes' of various sorts; the neural drive is altered. In particular the individuals often suffer from loss of memory and sometimes develop a morbid hunger. Thus Frazier [6] reports of one such man that he could eat 3 lb. of steak and 6 lb. of potatoes at a meal. Moreover, Fulton, Jacobson, and Kennard [8] observed a very similar excessive hunger in chimpanzees after removal of both frontal areas. Such evidence is of a crude type, and it would be impossible to maintain that we understand this sort of motivation at all fully. But it is clear, even from such simple experiments by removal, that the activity of some parts of the brain alters the motivating system, not only in simple ways, as by increasing or decreasing appetites, but also by controlling those much more subtle forms of motivation which express themselves as the personality of an individual.

This brief and superficial analysis of the functioning of the higher nervous centres is intended to show how they play a major part in enabling the animals which possess them to maintain themselves in unstable equilibrium with their environment by 'seeking' those sources of material which are necessary for conservation. Animals without such centres can perform curious feats, but few of them and only under limited conditions. With some development of these centres in cephalopods and arthropods there appears the capacity to learn, and perhaps to perform acts of behaviour which require more complex drives than those provided by the internal and external receptors alone. In the vertebrates the development of these large masses of tissue has gone very much farther, giving the animal a matrix of interconnected neurons within which patterns of activity can be recorded. In such animals a small external change, a scent or a line, sets up impulses which because they discharge into a centre which is already active in a particular manner become clues leading to the development of patterns of behaviour which satisfy the needs of life in the most indirect ways.

As has already been emphasized, we know very little yet of the modes of functioning of these more interesting parts of the nervous system. But the results of combined anatomical and physiological studies are beginning to suggest the lines along which it may be possible to understand and control the springs of action of ourselves and other animals. Comparative study, undertaken not only for its own sake, but with a view to finding suitable material for the solution of fundamental problems, has already proved as valuable here as in other biological fields.

Summary

This analysis of the types of functioning of the nervous system, and especially of its more complex centres, is intended to show how organization of our knowledge about the nervous system can be achieved by considering the part which it plays in enabling animals to maintain themselves in dynamic equilibrium with their environment. Ecological, physiological, histological, and physico-chemical investigations can thus meet in the combined study of the essentially morphological problem of finding how the organization of living systems is preserved.

The part played by the nervous system in this preservation is at first that of a *connector*, by which *receptors*, responding to changes in the surroundings, transmit messages to *effectors* which release energy in ways appropriate for self-maintenance. Behaviour in such animals is said to be the product of the *drive* or *motivation* produced by discharge of the internal and external receptors in response to changes within or around the animal.

During the course of the evolutionary history of animals the neuromuscular system has become more complex, enabling some later organisms to maintain themselves by special mechanisms in environments which their ancestors could not occupy. These changes in the organization give to the animals which we call 'higher' the following, among other capacities. 1. That of responding to aspects of environmental changes, such as those of direction or pattern, which are not distinguished by the simpler organisms. 2. Capacity of the effectors to respond not only as a whole motor mechanism for carrying the organism to areas where raw materials are available, but

by handling the environment with special and largely independent movements of the various parts to bring the tissues into conditions necessary for their maintenance. 3. Increased complexity of the central nervous system accompanies both of the above developments. The primary receptor centres, for instance, appear as regions allowing for the interaction of messages from different parts of the receptor field. This increased complexity of interaction between the messages coming from various parts of the body is made possible by the development of large and centralized as opposed to diffuse nervous systems. 4. The large masses of nervous tissue come to be continuously active, the neurons probably re-exciting one another in regular ways and thus building up a pattern of activity which continues for considerable periods of time. The existence of these continual activities may be the factor which makes it possible for the effects of past activity to influence present behaviour, that is to say for learning to take place.

In the supraoesophageal ganglia of cephalopods there are neurons so arranged that self-re-exciting chains of activity of the above sort could be set up. Optic and visceral sensory fibres converge on to these same neurons, which activate each other in a circular manner and thus provide a possible mechanism for the establishment of conditioned reflexes (p. 195).

The influence of these continuously active centres makes the nervous system the main agent in controlling the behaviour of the animals which possess them. It is this type of *neural drive* which makes it possible for the organisms such as man to obtain the raw materials necessary for their life in such indirect or 'improbable' ways.

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THE EVOLUTION OF THE CYTOPLASMIC APPARATUS OF THE CELL

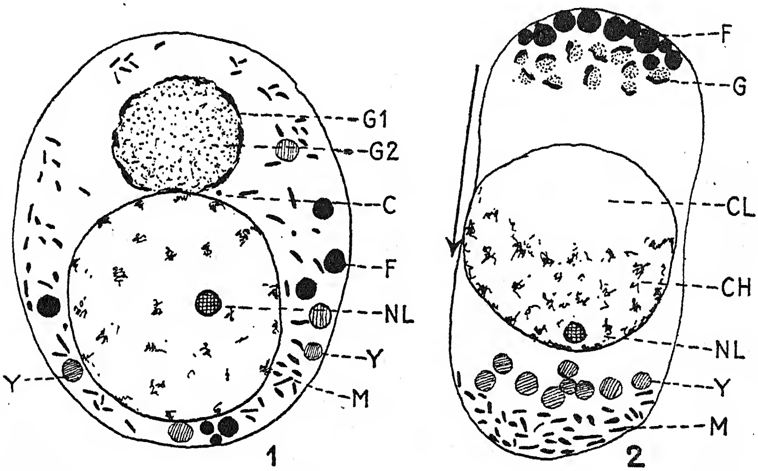
By J. BRONTË GATENBY

'We may agree that in any given cell or living organism, simple or complex in structure, all the parts are equally "living", and equally indispensable for the maintenance of life, or at least the continuance of the vital functions in the normal specific manner, without losing the right to inquire which of those parts are the phylogenetically older.' E. A. Minchin [18].

IT is now seventy years since the Golgi apparatus and mitochondria were discovered by Adolph Johann Hubert Freiherr von La Valette St. George, director of the Anatomy Institute of Bonn University from 1875 to 1906 [8].

A large amount of work has recently been carried out on the structure and arrangement of the cytoplasmic bodies in both protozoan and metazoan cells. It is the purpose of this essay, necessarily short in length, to endeavour to draw some conclusions from the results already obtained as to the possible line of evolution of the cell. It is obvious that the cells of the Metazoa are all arranged on the same basic pattern, so far as their outward nuclear and cytoplasmic appearance is concerned. The experienced cytologist can usually recognize the special type of cell found, say in the coelenterate or the arachnid. The differences in arrangement of basic structures in the nucleus and cytoplasm of various cells of Metazoa are so slight as to enable us at once to draw a universal metazoan cell. It is of course obvious that we are not here dealing with histological differentiations, which, however, in every case, can be traced back to the metazoan cell given here in Fig. 1. The nucleus contains one or more nucleoli (*NL*) and chromatin material or blocks floating in the karyoplasm, and, so far as we can ascertain, nothing else. In the cytoplasm is a large juxtanuclear Golgi apparatus consisting of a sphere (*G* 2) covered by a mainly lipoid cortex (*G* 1) which is always osmiophile. In the general ground cytoplasm are found mitochondria (*M*), centriole (*C*), fat (*F*), and various yolky bodies (*Y*). In the plant cell, mitochondria and Golgi bodies (osmiophilic plate-

lets of Bowen) are also present, as well as plastids, and other formed bodies peculiar to certain plant cells. When the metazoan cell is ultra-centrifuged [1], these bodies take up the positions shown in Fig. 2. Sudanophile fat (*F*) is the lightest, the Golgi bodies, now broken up into several pieces, come next, then usually below is the nucleus, which shows a



FIGS. 1 and 2. Typical undifferentiated animal cell in Fig. 1, strongly centrifuged in Fig. 2.

Letters: *G* 1, *G* 2, chromophile and chromophobe parts of Golgi apparatus. *C* 1, centriole; *F*, fat; *Y*, yolk; *M*, mitochondria; *NL*, nucleolus; *CL*, clear layer of nucleus; *CH*, chromatin.

clear area above (*CL*) of karyoplasm, the chromatin being forced down into the lower part of the nucleus, with the nucleolus heaviest. Sometimes the nucleolus passes through the nuclear membrane and lies below the nucleus in the cytoplasm. The heaviest cell inclusions are the mitochondria (*M*), yolk usually lying above them (*Y*). In the plant cell, such as that of the root tip of wheat or the bean, exactly the same relations are found [2].

Within the last ten years another cell inclusion, the 'vacuome', has been claimed to be present. This 'vacuome' is supposed to be associated in some way with the Golgi apparatus to form a Golgi zone, and is revealed, so it was said, by staining in the dye neutral red. No such fixed structure as the 'vacuome'

exists in animal cells. It is true, however, that neutral red often stains certain vacuoles or granules (Ehrlich) which appear to contain enzymes (Koehring), and in other cases is segregated in newly formed droplets in the living cell often in the region of the Golgi apparatus.

Some years ago neutral red cytology consisted of placing organisms or cells in a weak solution of the dye, and describing the red globules so produced as the Golgi apparatus. There is, however, a small number of accounts by competent investigators, who have claimed that the true Golgi apparatus apparently does stain red in this dye. Probably all of these cases can be explained by the fact that the contents of Golgi vesicles (in oogenesis) or the chromophobe part of Golgi bodies in neurones or gland cells, become loaded with a substance which stains in the dye. For example this is what happens in *Helix* neurones (W. Boyle [3]). Staining by neutral red of the unchanged osmiophile substance of the Golgi body never occurs in the vital condition. Neutral red in the lethal stages of the staining of a cell does, however, colour various cytoplasmic and nuclear bodies, including the dictyosomes, for example in *Helix* cells. It is not proposed here to go any farther into the questions of neutral red staining. It is sufficient to say that such work is interesting from the point of view of vital staining, but of little value in considering the Golgi apparatus and mitochondria.

Regarding the identification of various bodies which has been provided by the ultra-centrifuge, it is interesting that in all cells so far studied the Golgi elements are lighter than the mitochondria. Except for such material as starch granules, plastids, and heavy proteid granules impregnated with glycogen, the mitochondria are always the heaviest. In metazoan tissue cells, the mitochondria almost invariably are the heaviest structures in the cell. In mollusca, where the Golgi bodies are thick dictyosomes, the difference in specific gravity between them and the mitochondria is not great. These relationships apply to such diverse cells as the sporozoan trophozoite, the oocyte of *Gasterosteus*, and the endometrial cells of *Cavia*. This being so, the way is clear for biochemical study of large quantities of Golgi or mitochondrial material, collected by centrifuging mashed organs.

It should be noted that the writer's conception of the structure of the Golgi apparatus is that of a chromophile material (argentophile or osmiophile) which is very often attached to a non-staining or chromophobe material. The former is of a lipoid nature, the latter non-fatty and probably protein. The chromophobe material cannot always be made out, and is at its highest state of development in the male germ cells (spermatocytes and spermatids), where it has been recognized for generations under the name 'archoplasm'. In the egg cell it is often difficult to find a chromophobe substance, but in such eggs as those of the Oligochaeta the two parts are very clear.

The chromophile substance may exist in the form of batonettes, vesicles, or scales in the same cell, and can be seen *intra vitam* especially well in mollusc and insect germ cells (La Valette St. George [32]). This fact alone makes us disbelieve any hypothesis which assumes that the chromophile substance is artificially produced by silver or osmic techniques.

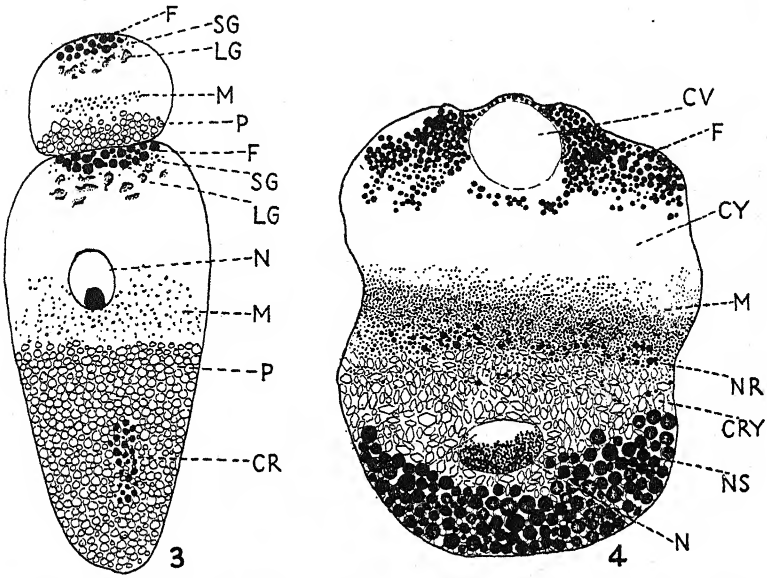
For the purposes of this present review the cell may be taken as depicted in Fig. 1, and its various physiological manifestations may be assumed quite safely to centre around the five parts already noticed, namely, nucleus, ground cytoplasm, Golgi apparatus, mitochondria, and, finally, centriole.

The task set is to find out, if possible, how this universal metazoan cell became evolved. It is present, as has been said, in the higher plants. Is it present in the Protozoa? The answer may be given immediately, that except for the Sporozoa (Hirschler), this type of cell is not typically present. In the Sporozoa some interesting work on the cell inclusions has recently been carried out by Miss M. Daniels [6], who has used the ultra-centrifuge in her investigations on three species of *Gregarina*. The cytoplasmic bodies known to occur in Sporozoa are paraglycogen, chromidial granules, mitochondria, fat, and Golgi bodies, and they centrifuge as shown in Fig. 3.

This is a remarkable demonstration not only of the Golgi bodies of a protozoon, but of the relative specific gravities of the various inclusions, for in both the protomerite and the deutomerite the inclusions take up identical positions.

When the trophozoites are removed alive from the ultracentrifuged gut of the *Tenebrio* larva, and placed in neutral red solution, and while still in the condition shown in Fig. 3,

neutral red globules appear soon throughout the whole organism, and not in the regions into which the Golgi bodies have been centrifuged. The Golgi elements do not therefore stain intra vitally in this dye as has been suggested by Joyet-



FIGS. 3 and 4. Strongly centrifuged Protozoa, showing stratification of cytoplasmic elements. Fig. 3, *Gregarina* from mealworm gut; Fig. 4, *Amoeba proteus*. Lettering: *SG* and *LG*, fine and coarse Golgi bodies; *P*, paraglycogen; *CR*, chromatoid bodies; *N*, nucleus; *CV*, contractile vacuole; *CY*, clear cytoplasm; *NR*, neutral red staining globules; *CRY*, crystal inclusions; *NS*, nutrient spheres; other letters as before.

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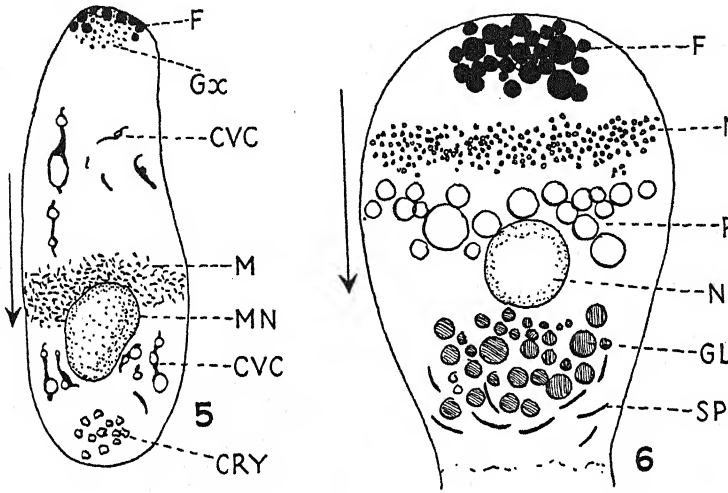
Lavergne. From work [15] previous to that of Miss Daniels, we know that the Golgi bodies spread out in the growing trophozoite in the manner found in metazoan and sponge oogenesis, and undergo definite dictyokinesis (even distribution of dictyosomes during cell division). Joyet-Lavergne describes the attachment of Golgi bodies on the anterior part of the microgametes of *Aggregata eberthi*, in the region of the acrosome of metazoan spermatozoa.

We can safely conclude that a characteristic Golgi apparatus is present in Sporozoa, and we may turn to the more

difficult task of examining the evidence from other groups of Protozoa.

Quite recently two members of the Sarcodina, *Amoeba proteus* and *Nebela collaris* (*pro parte*, Leidy), have been examined in this department, the former species by B. N. Singh, the latter by Mrs. Lamont (Miss R. MacKinlay). In *Amoeba*



FIGS. 5 and 6. Strongly centrifuged Protozoa. Fig. 5, *Paramecium* from data supplied by R. Brown; Fig. 6, *Nebela*, from data supplied by Mrs. Lamont.
Lettering: *Gx*, possibly Golgi bodies, but more likely fat; *CVC*, broken-up canals forming blebs; *MN*, macronucleus; *FV*, food vacuoles; *GL*, glycogen-containing granules; *SP*, shell plates; other letters as before.

proteus, which has also been studied by S. O. Mast and W. L. Doyle [17], the sudanophile fat, as usual, passes to the centripetal end of the organism, while the mitochondria occupy a band separated from the fat by an area of clear cytoplasm (*CY* in Fig. 4). Below the mitochondria are the heavier layers formed of neutral red staining granules (*NR*), crystals (*CRY*), and nutrient spheres containing glycogen. No homologue of the Golgi apparatus is known in *Amoeba proteus*. In *Nebela* the layers are shown in Fig. 6, namely fat (*F*), mitochondria (*M*), food vacuoles (*FV*), and finally glycogen-containing bodies. Here also no Golgi apparatus can be found. It may be asked, are not the neutral red granules of *Amoeba* the representatives

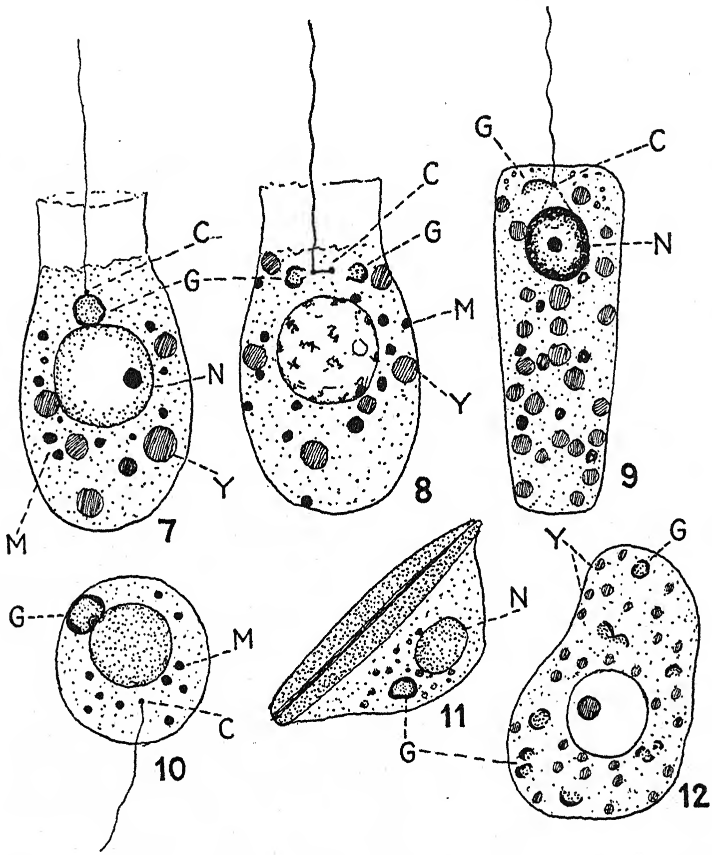
of the Golgi apparatus? Neutral red stains vitally so many diverse bodies that one should not be surprised if it did stain up Golgi bodies in some organisms, but in this case the neutral red bodies do not respond to the usual silver and osmic Golgi methods, have not the morphology of Golgi bodies, and do not occupy the same region of the cell in centrifuged organisms. Mast and Doyle identify an outer layer of the nutrient spheres (*NS* in Fig. 4) as Golgi bodies. At the present moment it is felt that Mast and Doyle's views on the identification of Golgi bodies in *Amoeba* will need to be supported by further evidence. From the work of Singh and Mrs. Lamont, we must conclude that the Golgi apparatus is absent in *Amoeba* and *Nebela*.

In 1923 the writer brought forward the hypothesis that the Golgi apparatus had originated in some primitive flagellate, in connexion with the flagellum-centriole complex. From 1925 onwards Duboscq and Grassé in a series of interesting papers asserted that the parabasal granule (kinetonucleus, kinetoplast, &c.) which usually lies at the base of the flagellum, was the homologue of the Golgi apparatus of higher forms. In 1933 Duboscq and Grassé published an exhaustive treatise on the parabasal bodies of flagellates [9]. It is not possible here to give an account of these researches, or of the various difficulties which the authors have encountered in developing their important theory. It is obvious that, especially in parasitic forms, the original simple parabasal has become developed along very diverse lines. This might be taken to explain the peculiar microchemical behaviour of the kinetoplasts of highly specialized flagellates as *Trypanosoma*, referred to below.

Concerning the relationships of the cytoplasmic bodies in flagellated and non-flagellated cells within the same organism, no better could be done than first to examine the case of sponges, where work on this aspect has been carried out by Robertson and Minchin,[1] Hirschler, Gatenby, O. Duboscq, and Mlle O. Tuzet. In the flagellated cell (Fig. 7) the Golgi apparatus lies in close topographical relationship to the centriole flagellar apparatus, and to the collar region of the cell. So far as is

[1] Muriel Robertson and E. A. Minchin [27] were the first to depict the Golgi apparatus of sponges. It is drawn by them in Pl. 25, Figs. 2, 3, 7, 34, &c., and they say, 'In the direct line between nucleus and blepharoplast, there is generally to be seen a vacuole, which has finely granular contents, and sometimes a minute central granule. Its significance is doubtful.'

known, the choanocyte Golgi apparatus never wanders away from this region, and practically always is in contact with the base of the flagellum. Turning to the newly metamorphosed

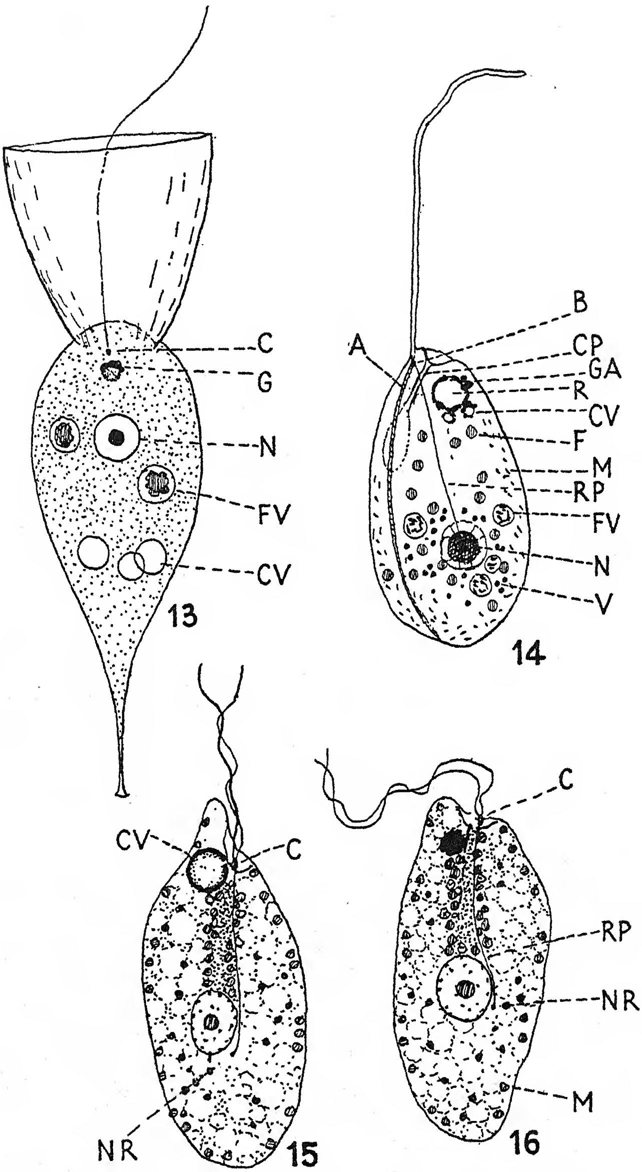


FIGS. 7–12. Sponge cells, from the works of Robertson and Minchin, Hirschler, Gatenby, Grassé, and Tuzet. Figs. 7 and 8, choanocyte, resting and in prophase of division. Fig. 9, flagellated cell of amphiblastula (Tuzet). Fig. 10, spermatid. Fig. 11, silicoblast, and Fig. 12, oocyte. Letters as before.

flagellated cell of the amphiblastula (Fig. 9), we find a crescentic or scale-like dictyosome (Golgi body, *G*) associated with the centriole, which is itself linked to the nucleus by a rhizoplast, strongly recalling the appearance found in certain flagellated Protozoa (Grassé, Duboscq). In the non-flagellated somatic cells of sponges, a typical eccentric juxta-nuclear Golgi

apparatus is found (Fig. 11, silicoblast), not different in appearance, position, or microchemical reactions from that of metazoan cells. The similarity is further demonstrated by the formation of the acrosome in spermatogenesis from this Golgi dictyosome (Fig. 10), and the spreading out of the dictyosomes in the usual manner in the eggs of higher forms (Fig. 12). Finally, in the granular cells of the amphiblastula, from being at first scattered in the cytoplasm, the Golgi element or elements come into close contact with the nucleus, as happens in the embryogeny of higher animals (e.g. Mollusca). We can therefore say definitely that there is a typical Golgi apparatus in sponges, which in the somatic and generative cells closely resembles that of higher animals, and, let it be stressed, in the flagellated cells comes into direct topographical relationship with the centriole flagellar apparatus (Figs. 7 and 8).

In Fig. 13 is a diagram of a choanoflagellate, based on the work of Saville Kent [14] and Henri de Saedeleer [28]. Here there is an osmiophile Golgi apparatus (*G*), consisting of chromophile and chromophobe parts, and related topographically to the centriole and flagellum as in the sponge. In these organisms one or more contractile vacuoles are found situated in the base of the cell, quite certainly unrelated to the basal body or Golgi apparatus. Although there is at present no information on the subject, it is likely that the basal body or Golgi apparatus of choanoflagellata behaves during mitosis like the Golgi apparatus of higher forms, both daughter organisms obtaining a moiety of the original body (Fig. 8). There is still no consensus of opinion as to the reason for the presence of the Golgi apparatus in the region of the base of the flagellum in such cells as the choanocyte and the choanoflagellate. The topographical relationship is not necessarily always very close, but in such cells the basal body is never outside that region of the cell from which the flagellum protrudes. Since during dictyokinesis the Golgi body divides under the influence of the centriole, and consequently at telophase is left in the region of the centriole and base of the flagellum, the topographical relationship may be due to this, and not to a function connected with the continuous movement of the flagellum. In the choanocyte and choanoflagellate the Golgi body is almost invariably single. If it moved away from the zone of the spindle it might



FIGS. 13–16. Protozoa from Saville Kent, de Saedeleer, Nassonow, Gatenby, and B. N. Singh. Fig. 13, Choanoflagellate. Fig. 14, *Copromonas*. *B*, basal granule of flagellum; *CP*, cytopharynx; *GA*, Golgi apparatus and contractile vacuole reservoir (*R*); *CV*, contractile vacuole; *F*, fat; *M*, mitochondria; *RP*, rhizoplast; *FV*, food vacuole; *N*, nucleus with central body; *V*, volutin. Fig. 15, *Chilomonas*. *CP*, cytopharynx; *RP*, rhizoplast; *CV*, contractile vacuole in diastole. Fig. 16, *Chilomonas*, vacuole in systole.

during cell division pass whole to a daughter cell. In view of this it would be inadvisable to bring forward the obvious hypotheses as to possible chemico-physical contributions of the Golgi apparatus to the kinetic functions of the flagellum. According to Duboscq and Grassé, parabasals appear to be absent in a large number of the Polymastigina. But if we assumed that the osmiophile cortex of the contractile vacuole represented the parabasal, the Polymastigina might come into line with other flagellates.

Recently Singh and the writer have paid some attention to the problem in *Copromonas*. According to the description given by C. Dobell thirty years ago [7], *Copromonas* is a fairly simple monad with a single flagellum, contractile vacuole and reservoir, blepharoplast, and nucleus. Wenyon [33] has recently given a more accurate description of this interesting organism, correctly describing the intra-nuclear central body. We find, however, that in *Copromonas* the reservoir may be extremely osmiophile, and its cortex breaks into two during the division of the organism in the manner of the parabasals of certain of the simpler parasitic flagellates. The reservoir at systole tends to be like a solid parabasal, and at diastole resumes its hollow condition. Singh and the writer have concluded that the osmiophile substance of the reservoir wall and contractile vacuoles is the homologue of the metazoan Golgi apparatus. Therefore in *Copromonas* a Golgi apparatus consisting of a permanent osmiophile material is always demonstrable, and associated with one or more smaller non-permanent contractile vacuoles which empty into the reservoir, and which, so far as we know, always have osmiophile walls. The substance of the walls (parabasal, Golgi apparatus material) passes intact into the cysts, as is known to occur in the case of the parabasals of other encysted flagellates. In *Euglena* a similar state of affairs appears to exist, an osmiophile wall having been demonstrated by Sigot[1] [29] and Miss Patten and Beams [25].

Concerning function, the parabasal has been regarded by some as an organ of pure secretion, by others as a structure in some way providing energy material for the flagellum, or as a sort of reservoir for the development of new parts of the neuromotor system.

[1] There seems to be confusion in the use of the terms reservoir and contractile vacuole. Sigot's osmiophile bodies surround the latter, not the reservoir.

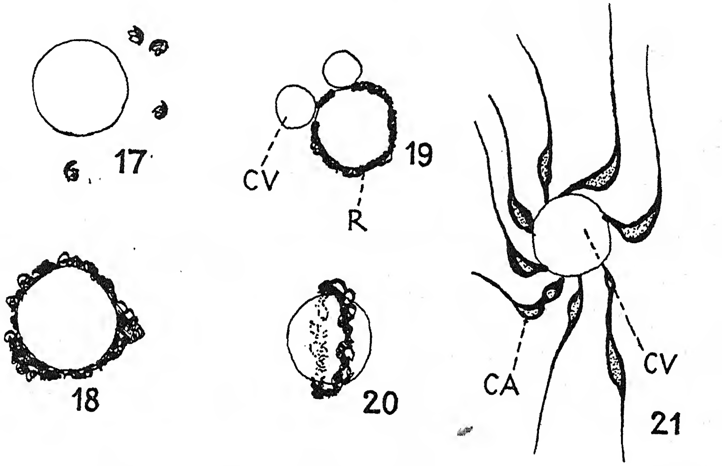
In at least two flagellated organisms appropriately examined, namely, *Trypanosoma* and *Leptomonas*, the parabasal stains positively with Feulgen's Nuclealfärbung reaction. Lwoff [16], in *Leptomonas*, says that the parabasal has a cortex with a positive thymonucleic reaction, and a medulla of probably a lipoid nature. In the metazoan Golgi apparatus the cortex is lipoid, and the medulla, where present, probably proteid in nature. We are unaware of any case where the metazoan Golgi apparatus stains in Feulgen, nor can the Feulgen reaction be depended upon implicitly.

In recent years various authors have reviewed the interesting theories of Nassonow with reference to the supposed homology between the protozoan contractile vacuoles with the metazoan Golgi apparatus. In *Paramecium* osmiophile canals can easily be shown by leaving the organisms in 1 per cent. osmic acid for a few days in an incubator at 22° C. Such a rosette of canals is shown in Fig. 21. Lest it be rashly assumed that these canals are artefacts caused by the osmic acid, it may be pointed out that R. Brown working in this department has shown that in ultra-centrifuged *Paramecia*, the canals can be found broken up into fragments (*CVC* in Fig. 5) which continue excreting so as to form the blebed structures depicted in the figure. As a matter of fact, previous to the work of Nassonow, it had been known that the canals of *Paramecium* were much longer than depicted in the inadequate diagrams found in zoology text-books. Nassonow showed that in such forms as *Chilomonas* among Flagellata, and in *Nassula, Lionotus, Chilodon* (holotrichous ciliates), and *Dogielella* (astomate ciliate), a contractile vacuole existed in the form of a vesicle with osmiophile walls, or an osmiophile halo (*Dogielella*).

The position and osmiophility of these contractile vacuoles in Flagellata like *Chilodon* so closely recalled the known Golgi bodies in the sponge choanocyte as to appear to justify a homology between the two structures.

Remembering, furthermore, that the function of the Golgi apparatus of metazoan gland cells had already been suggested to be excretory or secretory, the homology appeared strengthened. But when it was pointed out by various authors that in such organisms as *Amoeba* [17] and *Blepharisma* [19] the contractile vacuole had no thick osmiophile cortex, the homology seemed

less likely. As a matter of fact, there are at least four main types of contractile vacuoles found in Protozoa. Firstly, the type such as in *Amoeba* and *Blepharisma* (Fig. 17) certainly with no thick osmiophile cortex, and able, as shown experimentally by Miss Imogene Moore, to arise anew after the old vacuole had been cut out of the living organism [19]. Second, there is the type found in *Campanella*, *Zoothamnium*, *Vorticella*, *Epistylis*, *Nassula*,



FIGS. 17–21. Various types of contractile vacuoles. From Imogene Moore, Nassonow, Gatenby, and Singh. Fig. 17, *Blepharisma*. Fig. 18, *Chilomonas*, *Vorticella*, &c. Fig. 19, *Copromonas*. Fig. 20, *Nassula*. Fig. 21, *Paramecium*.

Lionotus (Ciliata), and in *Chilomonas*, in which the vesicle is surrounded by a thick osmiophile cortex (seen in optical section in Fig. 18). A peculiar variation of this is the halo or ring type described by Nassonow in *Chilodon* and *Dogielella* (Fig. 20). Third, there is the *Paramecium* type with complicated osmiophile canals entering a contractile vesicle without a lipoid cortex (Fig. 21), and lastly, the type found in *Copromonas*, where both reservoir with or without osmiophile wall and one or more osmiophile contractile vacuoles exist side by side (Fig. 19). Now when it is stated that the homology between metazoan Golgi apparatus and protozoan contractile is or is not possible, it is well to consider more fully what is meant. Is the homology between the vesicle without osmiophile walls, or between the lipoid cortex, halo, or canal—and the metazoan Golgi apparatus?

Is there any structure other than the contractile vacuole and

its parts present in Ciliata which could be urged as the homologue of the metazoan Golgi apparatus? The paper by Richardson and Horning [26] seemed to give us exactly what was wanted. These observers described in both *Opalina* and *Nyctotherus* 'polymorphic Golgi structures' which they stated were revealed in a definite manner by silver techniques. In this laboratory Miss Ruth Patten [25] failed to produce preparations similar to those of Richardson and Horning, except that in *Nyctotherus*, what were considered to be impregnated bacteria produced a picture somewhat like the Golgi elements of the Australian workers. The position here therefore still requires further elucidation,[1] especially in ciliates other than those in dispute. In the case of *Paramecium*, R. Brown, working with the ultra-centrifuge, failed to find a convincing Golgi apparatus. In Fig. 5, at *Gx* are shown some small granules, which certainly occupy the right region of the centrifuged organism, but with which, at present, neither Brown nor the writer feel satisfied. These granules may be ingested fatty particles from some other organism.

In *Blepharisma* Miss Imogene Moore [19] states that a Golgi apparatus other than the contractile vacuole exists. Now, study of an organism like the choanoflagellate (Fig. 13) seems to show that we cannot homologize the contractile vacuole and the metazoan Golgi apparatus. Moreover, in *Amoeba* and *Blepharisma*, for example, there is no cortex comparable to what exists in *Zoothamnium*, *Vorticella*, or *Lionotus*. We cannot accept such a hypothesis in that form, simply because it does not cover the facts. If, however, we assume that the contractile vacuole and the Golgi apparatus arose independently in the evolution of the cell, and that they became associated in certain organisms, it appears possible to bring into line the work of Nassonow, and that of Grassé and Duboscq.

In *Blepharisma*, and for that matter in *Nyctotherus*, scattered Golgi bodies without association with the contractile vacuole have been described. No satisfactory Golgi bodies have been found in *Paramecium*, or such forms as *Vorticella*, where there is definitely either a system of canals, or a thick lipoid cortex.

[1] Recently Miss Browne has shown that in *Spirostomum* the arrangement is a contractile vacuole without osmiophile walls, and quite normal Golgi bodies scattered in the cytoplasm.

If indeed an association between primitive Golgi material and contractile vacuole has occurred, this must first have happened in those flagellates in which the contractile vacuole is found in the anterior end of the cell. *Copromonas*[1] might be taken as an example of one stage in the evolution of contractile vacuole and Golgi apparatus.

Within the Parazoa a transition can be seen from a parabasal, such as the dictyosome of the flagellated cells of the amphiblastula undoubtedly is, to a typical Golgi apparatus of both egg and sperm cells. From the sponge parabasal we can pass to the protozoan flagellate parabasal, and from the latter to a contractile vacuole, the walls of which, in systole, represent a Golgi apparatus.

There are difficulties however. Why is the metazoan Golgi apparatus so often the site of the segregation of neutral red, and the contractile vacuole never? What is the purpose of the osmiophile basal substance known as the parabasal? If it were at first connected in some way with the working of the flagellum, how could it carry out this function after it has become either a reservoir or a contractile vacuole? If, for example, its function lies in the secretion of glycogen or a related storage substance for the use of the organism, is it likely that the contractile vacuole would have become associated with it? If, however, we assume, as seems possible, that the original osmiophile parabasal was an active area (acceptor) connected with the elimination of waste products at this energy centre of the organism, a union with the contractile vacuole would be an advantage to the protist.

If we adopted the view that one function at least of the Golgi apparatus of metazoan cells was to concentrate, by partial dehydration, the secretory materials originating either from the ground cytoplasm or from mitochondria, this would bring into line the duplex contractile vacuole and the metazoan Golgi apparatus. A survey of the known or supposed activities of the Golgi apparatus of metazoan cells, in the light of this suggestion, cannot be undertaken now, but it may be said that while there are certain difficulties, this hypothesis would fit in well with what is known of the behaviour of the Golgi bodies in metazoan gland cells and eggs, at least.

[1] A paper on the Golgi apparatus of *Copromonas subtilis* Dobell, is in course of publication.

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BACTERIAL STRAINS, AND VARIATION

By H. G. THORNTON

ANY discussion of bacterial strains must include some indication as to what bacteriologists mean by a bacterial species, of which these strains are subdivisions. This, however, is a subject about which the bacteriologist is cautiously vague. He is filled with envy at the comparative ease with which higher animals and plants can be classified. Their systematic position is determined by morphology alone; comparative physiology would be further advanced had this not been the case. A higher animal can even be identified when it is dead. Such is not the case with bacteria. Their anatomy, as far as it can be seen under the microscope, is too simple to afford a basis for any but the most generalized grouping. It is not altogether easy to carry out even a generalized morphological grouping, because many bacteria show marked changes in morphology not only in different environments but even during the course of growth on a single medium. We are therefore driven to use physiological characters, such as the biochemical changes produced in culture media, antigenic behaviour, and pathogenicity. Here we are really utilizing the enzymic structure, or, one might say, the micro-morphology of the organism, as is illustrated by recent work on the distribution of antigens in various parts of the bacterial cell. There is no general agreement as to how much relative weight should be accorded to microscopic appearance and to physiology in classifying bacteria. It seems rational to use visible characters such as cell shape in formulating major divisions.

By confining his attention to the most frequent cell type in a young culture upon a standard medium, the bacteriologist can usually place an organism in a definite morphological group. But the use, for classification, of physiological peculiarities easily detectable in culture has an obvious practical advantage to the laboratory worker, and it is not surprising that such striking performances as ammonia- or hydrogen-oxidation and nitrogen-fixation should have given the organisms

concerned an added prestige in the eyes of the bacteriologist, which has sometimes raised them to high systematic rank. Attempts have been made to divide most of the important groups of bacteria into species and strains according to the changes, such as carbohydrate fermentation, which they produce on various media. As a rule, the very multiplicity of possible chemical changes produced by any one organism, and their great variability in performance, make it impossible to arrive at a really logical classification by their help alone. Indeed, where cell appearance, and reactions on laboratory media, are the only criteria available, the bacteriologist's classification is apt to be largely a subjective process.

Fortunately there are two other types of character which enable some important groups of bacteria to be classified much more rationally. They are parasitism and antigenic behaviour. The infection of a specific host by a micro-organism, and the production in it of definable symptoms, often provides a means of identifying that micro-organism with certainty. The existing methods of serology enable bacteria to be grouped both into strains by means of highly specific antigens and into larger groups by means of less specific antigens.

Two examples may be given to show the use of these various methods of classifying bacteria into strains and species.

The assistance rendered to the systematists by host specificity is well illustrated by the familiar nodule-forming bacteria which infect leguminous plants. These bacteria form a group to which generic rank has been given under the name *Rhizobium*, which is defined by the fact that all its members produce nodules upon the roots of some legume, while nearly but not quite all possess the remarkable power, when within the host plant, of 'fixing' the free nitrogen of the soil atmosphere. The members of the genus possess in common certain features of cell morphology and certain growth characters on laboratory media, but it should be noted that neither its cytology nor its physiology will enable a member of the genus *Rhizobium* to be identified as such, if its capacity to form nodules is unknown. The genus has been divided into species or infection-groups, each of which infects only a certain group of host legumes (Baldwin and Fred [8]). These species can be identified not only by the host plants which they can infect, but also sero-

logically, by agglutination tests (Klimmer and Kruger [17]). In some cases there are also small differences in the shape of the bacterial cells. The cultures of nodule bacteria of a single species, or infection-group, can be classified more finely into strains which differ in various ways, most importantly in the efficiency with which they will fix nitrogen and benefit the host (Stevens [21]). Differences between strains also involve their behaviour on laboratory media, and their serological behaviour. These differences within the species are not always or even usually correlated, so that the same group of cultures isolated from one host plant can be arranged into different varietal groups according to the tests applied to distinguish them.

As a second example of classification we may take the pneumococci, for this group provides what is perhaps the best example of the use of antigenic behaviour to justify classification. The group has been given the specific name of *Streptococcus pneumoniae*, based on its pathogenic behaviour and microscopic characters, which are rather distinctive. The division of the group by serological tests was undertaken by Dochez, Avery, and their colleagues [12], who tested many strains and found that the great majority of them fell into three sharply distinct serological groups (types I, II, and III), while the remaining cultures differed amongst themselves. More recent work has confirmed the distinctiveness of these three now classical types and identified some twenty-nine other serological groups (Cooper and Walker [9]). The typical pneumococcus is endowed with a capsule composed of polysaccharide. Heidelberger and Avery and their colleagues [15, 16] isolated in a chemically pure state the capsular polysaccharides from types I, II, and III. Each type yielded a distinctive polysaccharide which gave a specific precipitation at high dilution with antiserum prepared against that particular type. The chemical investigation of the other twenty-nine antigenic types of pneumococci is not yet complete, but it seems likely that each will be found to have a distinctive polysaccharide in its capsule. Tillett, Goebel, and Avery [24] have isolated from the pneumococcal cell itself another type of polysaccharide which contains phosphoric acid. This also possesses antigenic properties but is not strain-specific; it seems rather to define *Streptococcus*

pneumoniae as a species. Avery and Heidelberger [6] have further discovered in the cell a nucleo-protein antigen which is shared not only by all strains of pneumococci but by other species of streptococcus. Thus we have, in the pneumococci, highly specific antigens by which strains can be separated, an antigen characteristic of the species, and a group antigen common to neighbouring species. This use of specific and group antigens, as aids to classification, is a contribution to systematic biology which is beginning to be appreciated but has not yet been sufficiently utilized by biologists in other fields.

Bacterial Variation

The study of bacterial variation was confused in its earlier stages by discussion as to whether bacteria possessed complex life-cycles like some of the protozoa and, if so, whether the variants recorded from time to time were not stages in some such cycle. The question of life-cycle is not yet fully settled, although the extravagantly complex life-cycles once proposed have been dispersed by the introduction of improved methods of pure culture from single cells. But some bacteria do undoubtedly pass through a cycle involving various types of cell, and different methods of reproduction. A simple cycle of this sort can be observed, for example, in the nodule bacteria (Thornton and Gangulee [23]), while reproduction by budding as well as binary fission has been shown to exist in *Bacterium malvacearum* (Stoughton [22]). But, such series of changes are very different in their nature from the sudden appearance in a pure culture of variant types that can be isolated and will maintain their new characters for a long or even indefinite period of sub-culturing. It is this tendency of many bacteria to produce striking and more or less stable variants that has proved a very fruitful field of study. At one time bacteriologists, when discussing the phenomenon, used terms such as 'mutation', having a fine genetical sound, but we have now been persuaded that such terms carry a dangerous implication of knowledge concerning the genetical make-up of the parent bacterial cell which we are very far from possessing. Non-committal terms such as 'dissociation' and 'variation' are now *de rigueur*.

Bacteria have been observed to produce variants in respect

of the shape of the cells, the appearance of growth in the mass, biochemical activity in laboratory media, pathogenicity, and antigenic behaviour. Variants often differ from the parent type in several of these respects. Thus, variations in cell structure and in the appearance of the colony are often associated with one another and with antigenic behaviour. Indeed, the critical study of bacterial variation has been closely related to the analysis of the antigen make-up of the bacterial cell. As long ago as 1903 Smith and Reagh [20] obtained a variant of the hog cholera bacillus which differed from its parent strain in being non-motile and without flagella. A serum prepared against the parent motile type was found capable of agglutinating both motile and non-motile types, but was much more active against the former. By exposing this anti-serum to an excess of the *non-motile variant* they were able to remove, by absorption, all the agglutinins capable of acting upon this variant, but found that the serum thus treated would still agglutinate the motile type. They concluded that, in the motile form, the possession of flagella was associated with antigens that were not possessed by the non-motile variant, and that were additional to those characterizing the body of the cell, which latter were common to both types. Similar results were obtained by Weil and Felix [25] working with a strain of *B. proteus* which gave rise to a non-motile variant. Here the loss of motility produced a striking difference in colony formation owing to the inability of the organisms to spread over the surface of the medium. More recent work has confirmed the fact that non-motile variants of a normally motile species have lost a highly specific group of antigens associated with the presence of flagella.

A most frequently occurring variation, now known in many different species of bacteria, also affects the appearance to the naked eye of the colony on platings. This was first investigated by Arkwright [2, 3, 4], who worked with bacteria of the typhoid group. The normal colony characteristic of this group is smooth and glistening. The variants in question produce rough granular colonies, and show correlated differences in their growth in liquid culture. The difference in colony appearance seems to be due to a modification in the process of cell division (Nutt [19]). In the 'smooth' type the cells

separate at once after division, whereas in the 'rough' type the cells remain attached for some while, so as to produce short chains. But here again, the change from 'smooth' to 'rough' type involves characters much more fundamental than the mode of division and resulting colony appearance. Thus, in pathogenic forms, the 'rough' variant is usually far less virulent than the 'smooth' type. The two types also differ markedly in their antigenic behaviour. The 'smooth' type is characterized by a highly specific reaction to immune sera, whereas the 'rough' type will generally react not only with a serum prepared against itself but also with sera prepared against the 'rough' forms of other bacterial strains. This is well illustrated by the critical study of the pneumococci referred to above. The typical capsulated pneumococci, with their very specific antigens, are of the 'smooth' type. 'Rough' variants of these strains which have appeared are found to be devoid of capsules, and of the strain-specific antigens associated therewith. But they retain a protein antigen that is common to the 'rough' forms of all the strains. The emergence of 'rough' variants, like that of non-flagellated forms, seems usually to imply the loss of some constituent of the bacterial cell that gives to the parent types their antigenic specificity. It has been found relatively easy to induce the appearance of 'rough' variants by subjecting a 'smooth' strain to unfavourable conditions for growth. But the reverse change from 'rough' to 'smooth' type is far more difficult to bring about.

When it is remembered that bacteria may, under favourable conditions, multiply several times in an hour, they might be thought good material to use in studying the mechanism of inheritance. Unfortunately they possess two serious limitations. In the first place, owing to their small size, we are quite ignorant as to the internal mechanism of cell division,[1] and we do not even know whether conjugation takes place. The second and almost more serious limitation lies in the difficulty in following the individual offspring of a given parent cell. We can isolate a single cell, allow its offspring to multiply, and perhaps re-isolate, from amongst the mass of its descendants,

[1] Bodies suggestive of nuclei, that divide before the cells do so, have sometimes been described, as in the case of *B. malvacearum* (*see* Stoughton [22]). But their small size approaches the limits of microscopic resolution.

some whose characters differ from those of the ancestral cell from which the culture started. But we know nothing of the exact genetical history of these new forms during the many generations that passed in the culture. It is as though a geneticist were able to work with his *Drosophila* only in mass culture.

The material provided by bacteria is perhaps better suited to study the action of selection upon a new type that may appear in a population. Variant forms are not often observed in very young cultures. The method of plating highly diluted suspensions, and examining a few hundred colonies, also prevents a variant from becoming apparent until this variant attains at least 0·1 per cent. of the population. It seems natural to suppose that the original variant must have competed successfully with the parent type and have increased its relative numbers in the population. There are some cases where the more rapid growth of the variant can actually be observed. The type of variant originally found by Massini [18] illustrates this. He found a strain of *B. coli*, originally unable to ferment lactose, whose colonies on lactose agar developed raised papillae due to more rapid growth of the bacteria at certain spots in the colony. These papillae were found to be composed of a variant form that could ferment lactose. Here not only was the increased growth of the variant relative to the parent form visible in the mass, but one can readily see where the new type had a selective advantage.

In many cases the appearance of variants in a bacterial culture is unpredictable and apparently haphazard, though one may, by suitable environment, improve the likelihood of their production. In the case of the pneumococci, for example, Dawson and Sia [10] found it possible to induce the development of 'smooth' variants of a given antigenic type by growing the 'rough' form in the presence of a heat-killed suspension of the 'smooth' type desired. Alloway [1] was able to bring about a similar apparently directed variation by supplying the 'rough' form with extracts of the particular 'smooth' type aimed at.

Some bacteria show a remarkably high rate of dissociation. Deskowitz [11] has investigated a remarkable series of unstable strains of bacteria belonging mostly to the species *Salmonella*

aertrycke which showed rapidly recurrent variation. Thus one of these strains on plating produced 'rough' and 'smooth' colonies. Isolations from the 'smooth' colonies remained true to type, but platings from the 24-hour-old 'rough' colonies always produced colonies of both types. The 'smooth' stable colonies were composed solely of short rods, while the 'rough' unstable colonies contained short rods and filamentous cells. Single-cell isolations from the latter always gave rise to a mixed population of rods and filamentous forms, while the short rods bred true. It would seem that the further investigation of such unstable forms which continuously and regularly produce variants, may lead us to some deeper knowledge of the mechanisms of bacterial genetics.

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LIFE-CYCLES OF CERTAIN INFUSORIA WITH OBSERVATIONS ON SPECIFICITY IN PARASITIC PROTOZOA

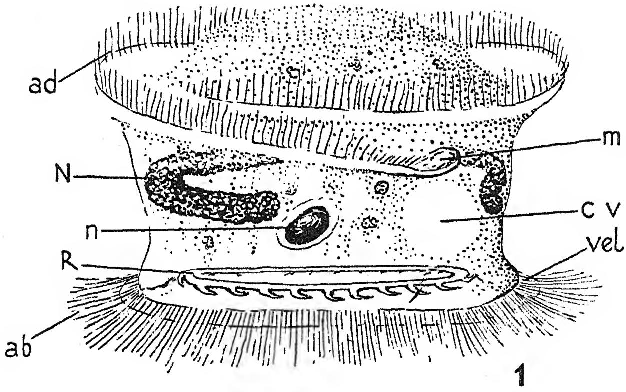
By HELEN PIXELL GOODRICH

MANY Infusoria recently studied show an unexpected complexity in their life-cycles, some forming interesting evolutionary series which may throw light on the difficult problem of the evolution of parasitism among Protozoa. It has often been suggested that commensalism marks the threshold of true parasitism. There are certainly living on well-known hosts many epizoic Infusoria about which there is some difficulty in determining whether they are commensals or parasites.

It is, of course, to be understood that a commensal or messmate shares the food of its host, its doing so being more or less a matter of indifference to the host. Sometimes the commensal may feed, as will be pointed out below, on a by-product, such as bacteria or yeasts growing on that food, and may thus act as a scavenger. On the other hand, a true parasite lives at the expense of its host by feeding on the fluids or tissues of its body. As it becomes more and more dependent on its host, so its own unused organs usually degenerate until we find that a long-established parasite has no organs of locomotion, no mouth, no contractile vacuole, and simply absorbs by osmosis nutritive fluids of its host.

Within the peritrichous genus *Trichodina* there does appear to be a definite transition from the one to the other mode of life.

T. pediculus (Fig. 1) is the well-known ciliate which moves slowly over the surface of *Hydra*, picking up odd scraps of food, bacteria, and any debris, thus acting as a scavenger. So early as 1886, it was shown by Rosseter [18] to be the same *Trichodina* as that on the gills of *Necturus* and the larva of another newt, *Triturus*. This was done by demonstrating that specimens were interchangeable from one of these hosts to another. These experiments were independently confirmed by Fulton [8] in 1923. There is thus no doubt that this species,



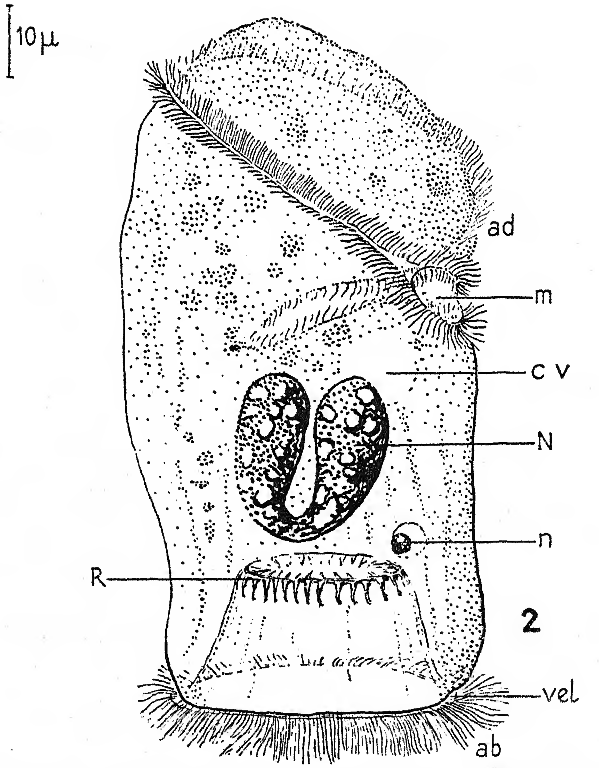


FIG. 1. *Trichodina pediculus*, from *Hydra*, drawn free-hand to same scale as 2.

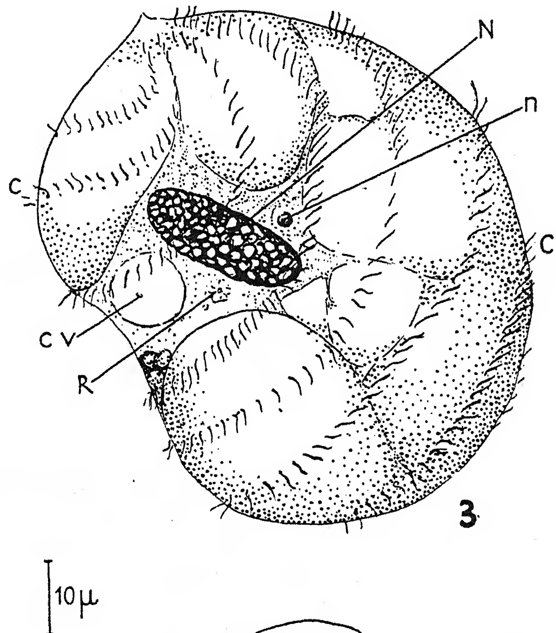
FIG. 2. *T. urinicola*. *ab*, aboral cilia; *ad*, adoral cilia; *cv*, contractile vacuole; *N*, granular somewhat horseshoe-shaped macronucleus; *n*, micronucleus; *m*, mouth; *R*, denticulated ring at inner end of sucking disk; *vel*, velum. (After Fulton.)

an epizoic commensal, has widely differing hosts. Fulton found another *Trichodina*, *T. urinicola* (Fig. 2), as an endoparasite in the urinary bladder of a moribund toad. He came to the conclusion that this was identical with a fairly common, though hitherto unnamed species, in the same site in the newt *Triturus*. Morphologically, it differs chiefly from *T. pediculus* in being taller and in having a more deeply invaginated sucking disk (Fig. 2, *R*). This sucker undoubtedly helps the ciliate to take a firmer hold of the bladder wall, an adaptation to its sedentary and parasitic mode of life.

Other *Trichodina* have been recorded from the body surface and gills of fish, also one from the bladder of a pike, but unfortunately little is known of their life-cycles. Fulton suggested that *T. urinicola* may have evolved from forms like *T. pediculus* infesting fish-like ancestors; the ciliates leaving the gills and body surface for the bladder as or before the host left the water.

To pass now to the consideration of some holotrichous ciliates. Much interesting work has recently been published by Chatton and Lwoff [3] and others on the many genera of the family Foettingeriidae. These Holotricha show a remarkable uniformity in main outline, notwithstanding their complicated life-cycles. The ciliation is reduced to a few meridional rows of cilia (always less than 22) showing at times considerable torsion (Fig. 3). They are, of course, heterocaryote, the macronucleus being often branched or reticulated. The mouth, placed ventrally, is minute, and leading to it is a characteristic special structure, the rosace, which probably provides a means of suction and filtration, since no solid food seems ever to be ingested. Chatton and Lwoff maintain that the nutrition of the whole family is essentially parasitic, although these ciliates are free in the water for a considerable part of their life-cycle and they retain a contractile vacuole. During the very active vegetative stage the ciliate rapidly absorbs food from its host and grows very fast, but never multiplies. As the food is digested it forms large, clear, and often coloured albuminous masses between the strands of protoplasm (Fig. 3). Then feeding and activity cease together and are succeeded by a division stage—the only one in the life-cycle. This takes place in the open water, generally under cover of a cyst wall, and a varying and often large number of small active ciliates are

formed. Chatton calls these 'tomites'—a useful word since it does not commit one as to whether these small ciliates are formed asexually (meronts or schizonts) or as the result of a sexual process such as has occasionally been recorded in



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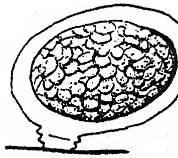

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FIG. 3. *Physophaga*, ventral view showing strands of protoplasm between the large clear blue masses of vitelloid substance. *C*, lines of cilia; *cv*, contractile vacuole; *N*, macro-nucleus; *n*, micronucleus; *R*, rosace.

FIG. 4. Stalked resting cyst of same. (After Percy.)

Foettingeriidae. On escaping from their cyst, they seek out another or the same host on which to form resting cysts (Fig. 4). From these small cysts the single young ciliate emerges at a time to fit in with the host's life-cycle.

Foettingeria itself (Caullery and Mesnil [2]) is well known as a parasite in the gastric cavity of most species of actinians.

The full-grown vegetative form is about 1 mm. in length and escapes into the sea where it forms a thick mucilaginous cyst on any convenient support, and then produces numerous tomites. These, as they escape from the division cyst, seek out one of several crustaceans on which they can form their resting cysts. For the cycle to be completed, the crustacean, together with its epizoic cysts, must be ingested by a suitable actinian, and while the crustacean is digested the cysts open. From each emerges the contained small ciliate which, after feeding for a few days, becomes full grown.

Another genus, *Physophaga* (Percy [14]), is restricted, so far as is known, to a single host species, but is not so definitely parasitic. Its vegetative stage is the beautiful blue ciliate (Fig. 3) which may be seen in the moults of *Gammarus pulex*, the freshwater shrimp. Here it swims rapidly about feeding on the exuvial secretion left by the departing host. The blue colour is derived from carotinoid albumens, the intensity varying with the nature of the shrimp's food. Upon emergence from the moult, the full-grown ciliates may be encouraged to encyst on suitable surfaces, even cover glasses. By setting the cysts up in hanging drops under the microscope, the process of division into 2–10 tomites may be watched through the thin transparent cyst wall. The first sign of activity is the vibration of the cilia of the tomites which soon afterwards begin moving round the inside of the cyst and their contractile vacuoles become active. On emergence they are 32–40 μ long and dash about seeking out freshly moulted shrimps on which to form stalked resting cysts (Fig. 4). Sometimes masses of these cysts are produced, overlapping one another on the sterna at the bases of the gills and appendages. By the time the host is ready to moult, signs of activity appear within the resting cyst, first the appearance and slow discharge of the contractile vacuole and then ciliary action. As soon as the moult takes place, the tiny ciliates become violently active, burst out of their cysts, and swim about inside the moult, feeding and growing with extraordinary rapidity during the few hours of their vegetative life.

It is interesting to note the time relation necessary here. The moults do not take place at very regular intervals, being less frequent as the shrimps grow older and liable to be delayed

from various causes, and yet these ciliates have to synchronize escape from their cysts almost to the minute to be able to complete their life-cycle.

Conjugation has been observed, and apparently the conjugants sometimes encyst together; but more observations are required on their further behaviour. Pairs may be easily distinguished when present in a moult for, as in other Foettingeriidae, there are never any specimens undergoing binary fission with which they might be confused. *Physophaga* was the first freshwater member of the family to be recorded: Chatton and Lwoff soon after described a similar, though generally colourless, ciliate from moults of *Asellus aquaticus* and named it *Oospira aselli*. In their 1935 monograph, however, they include these two freshwater forms in the genus *Gymnodinoides* established by Minkiewicz in 1912 for coloured ciliates found in the moults of Decapod Crustacea.

By employing their improved silver impregnation method, after wet fixation, these French biologists have been able to determine with great precision the remarkably constant arrangement of the cilia in all the members of this family.

One more genus of the Foettingeriidae that is specially interesting to us here is *Polyspira* (Minkiewicz [13]). This passes its vegetative stage in the moult of *Eupagurus* and forms resting cysts on its gills. It differs, however, from all other genera of the family in having no reproduction cyst, its adult vegetative form producing tomites by linear division or segmentation free in the sea. Now, this same curious reproductive process, reminding one of segmentation in Cestodes, has long been known in certain endozoic ciliates, for instance, *Chromidina* (Fig. 5), a true astomatous parasite of cephalopods. In 1908 Dobell [4] described the branching macronucleus of *Chromidina* which has some resemblance to that of *Foettingeria*. In 1928 Chatton and Lwoff made the important discovery that the tomites of *Chromidina*, formed by segmentation in the cephalopod kidney, may pass into the sea and remain mobile for 5 to 6 days. They concluded, therefore, that these were either the actual infecting stages or that they might attach themselves, as do tomites of *Foettingeria*, to some unknown secondary host destined to be eaten by the cephalopod.

There is evidently further interesting research to be done

on transmission in this genus, and also in *Opalinopsis*, another ciliate long known to infect cephalopods, together with *Chromidina*. The family Opalinopsidae (Hartog [10]) was established to include these two genera, both of which have branching macronuclei, and Chatton and Lwoff now unite it with the Foettingeriidae in the suborder Apostomea.

In this suborder, then, we can trace a gradually evolving parasitism: beginning with the scarcely modified blue ciliate which is almost free living—merely feeding on waste products of *Gammarus* left in its cast-off moults—we pass to *Foettingeria*, which obtains food and shelter in the gastric cavity of actinians, and thence to the astomatous and sedentary *Chromidina*, a true endozoic parasite. Further, the free-living tomite appears in the cycle of all the species—even the regressive *Chromidina*.

There are, of course, many other astomatous ciliates: the loss of the mouth being due to convergent adaptation rather than to phylogenetic relationship.

Closely connected with the Apostomea appear at first sight to be the Anoplophryidae which, as well as being astomatous, have similar segmentation and a macronucleus showing some tendency to branch. However, Chatton and Lwoff emphatically deny any real connexion, chiefly owing to differences in ciliation. To determine their true affinities, we shall have to wait till more is known of the life-cycles of these forms which have been recorded at intervals, though generally with the briefest details, since 1853.

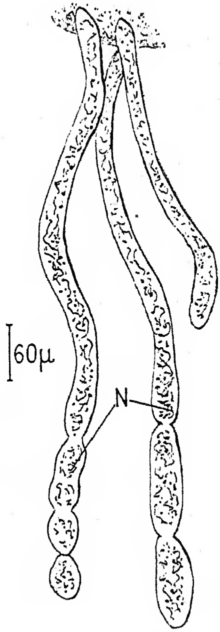

FIG. 5. *Chromidina elegans* attached to renal epithelium of Sepia showing segments at free ends of the two large specimens. *N*, branched nuclei. (Partly after Chatton.)

Another group of ciliates, in which can be traced stages in the evolution of parasitism, is that containing forms which attach themselves by means of special fixing or thigmotactic cilia.

Most of these ciliates live in the mantle cavity of bivalve

molluscs, frequently attaching themselves to gills, palps, or mantle, and feeding on such particles of food as they can obtain from the host's supply drawn in with the respiratory current of water. Chatton and Lwoff (1926) call the whole group Thigmotricha, and include in it four families, all of which, they maintain, are specialized Holotricha. These families are generally commensals, but one, the Sphenophryidae, is considerably advanced in parasitism. It contains the genus *Sphenophrya*, the adult of which has neither mouth nor cilia. Vestiges of cilia are represented by numerous basal granules,

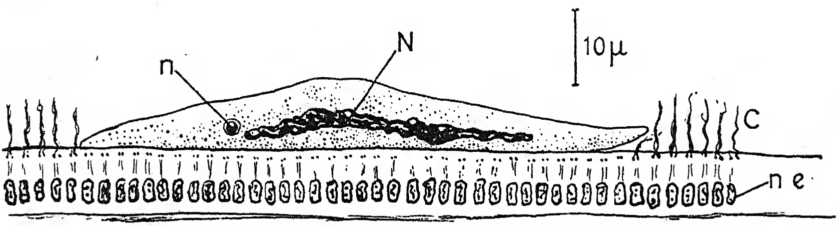

FIG. 6. *Sphenophrya* attached to gill of *Petricola*. *N*, macronucleus; *n*, micronucleus; *C*, cilia of gill; *ne*, nuclei of gill epithelium. Stained iron haematoxylin.

some scattered, others in rows forming a system of striations. There is also a silver line net-work, well shown by Chatton and Lwoff's special method.

Fig. 6 represents one of these curious creatures sent me for identification by Miss D. Atkins a few months ago. They were lying along the gill filaments of a piddock, *Petricola pholadiformis*. In such a position not only would cilia seem superfluous but even detrimental, since liable to be entangled with those of the host. Their favourite site on the gill is the region of the latero-frontal cilia, some of which are suppressed or destroyed by them. There can be no doubt that this species is a destructive parasite.

Food appears to be absorbed by osmosis along the attached side, which is flattened or even concave. The parasites when detached were carried passively by the currents set up by the host's gill cilia. They were in fact quite immobile at this stage, though Chatton records the formation of ciliated buds by means of which infection is spread, as in *Acineta*. Two other parasitic species of *Sphenophrya* have been recorded from

Finland, and one of them appears to be closely related to Miss Atkins's specimens. The latter are smaller (35–88 μ long) than any of the other three, but they are not budding and are possibly not full grown.

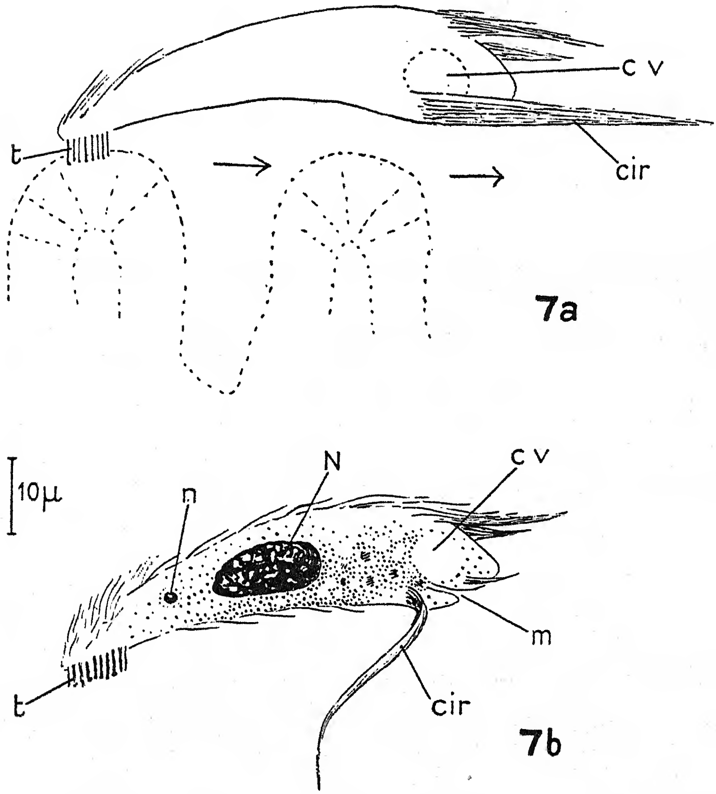

FIG. 7. A Thigmotrich from mantle cavity of *Pholas dactylus*, seen from left side.
a. From the living, attached to gill (dotted outline). Most of the cilia lie close against the body and are not shown.
b. Specimen stained in iron haematoxylin.
cir, ventral cirrus; *cv*, contractile vacuole; *N*, macronucleus; *n*, micronucleus; *m*, mouth; *t*, thigmotrichous cilia.

Although we have numerous preparations of this *Sphenophrya* both free and in sections of the gills, we still want more living specimens.[1] In looking for them, I found another piddock, *Pholas dactylus*, heavily infected with a Thigmotrich, which had

[1] A detailed account of this ciliate is to be published in the *Q.J.M.S.*

evidently only reached the commensal stage (Fig. 7). It had a mouth though it was rather reduced in size and, as is usual in Thigmotricha, it was near the wider end of the body which is posterior during movement. Just anterior to the mouth in this form is a bunch of long cilia only loosely attached to one another but forming a distinct ventral cirrus. It sometimes lashes vigorously, moving from its posterior position overlying the mouth (Fig. 7*a*) until it projects at right angles to the long axis of the ciliate's body (Fig. 7*b*). From the ventral region of the aboral end arise the special thigmotactic cilia, rather short and thick-set, capable of taking an astonishingly firm hold of the gill (Fig. 7) or other support. This end, of course, faces into the current formed by the gill cilia, and the thigmotrich's other cilia then lie as close to its body as possible, giving a distinct stream-lined effect (Fig. 7*a*). The dorsal cilia at the oral end often form a right and left cirrus, and another small one is just posterior to the mouth, where it may be hidden by the large ventral cirrus when projecting posteriorly. When the ciliate is detached its movements are rapid and jerky, direction changing frequently. Specimens dividing transversely may be seen swimming with the others.

This distinctive ciliate is perhaps more closely related to the Hypotricha than any of the other Thigmotricha; however, the cirri easily separate into their constituent cilia. Although some are distinctly longer than others, there is a fairly close covering of cilia in striations running obliquely backwards on the dorsal surface. Therefore it should probably be included in the family Ancistridae (Issel). Unfortunately, many new and incompletely defined genera have recently been placed here and I shall not, at present, attempt to identify this species further.[1]

Between the family Ancistridae and the Sphenophryidae mentioned above, Chatton and Lwoff place the family Hypocomidae (Bütschli) where the cilia may be reduced to a small thigmotactic field, but there is also a special sucker for fixation and food absorption. It is by the loss of this sucker and all cilia in the adult that the family Sphenophryidae, they suggest, has been evolved.

Chatton and Lwoff also found in a bivalve at Roscoff and

[1] A detailed account of this ciliate is to be published in the *Q.J.M.S.*

another at Wimereux a ciliate less sedentary than most Ancistridae. It led, in fact, a very active life in the pallial cavity, only occasionally fixing itself and generally appearing free like *Paramecium*. On close examination, however, it showed a small oval field where the cilia were longer and closer together than elsewhere. Further, the movements of these cilia were not synchronized with those of the rest of the body, being sometimes rigid while the Infusorian was swimming or showing waves of movement while it was at rest. That is to say, there was a true thigmotactic area, and they called this form *Thigmophrya bivalviorum* and created the family Thigmophryidae to contain it. This family then stands between the Ancistridae already very specialized and free normal Holotricha such as *Paramecium*.[1]

A remarkable evolutionary series is thus obtained from ordinary Holotricha with uniform ciliation as in *Paramecium* through *Thigmophrya* which anchors itself for short periods by means of a small thigmotactic area: thence to the definitely specialized Ancistridae, with reduced mobility, rather small mouths and gullets, and finally to such definite parasites as *Sphenophrya* with no mouth and complete immobility due to loss of cilia in the adult.

In concluding this brief review of a few life-cycles, it may be well to emphasize that during the life of an organism there is constant reaction of its inherited constitution to external conditions. Those individuals which respond favourably survive in the struggle. Thus the life-cycle is made up of those responses to environment which secure survival, and the evolution of a complex life-cycle results from the successive adaptations of the organism to changing external conditions. In so far as the environmental conditions are uniform, the life-cycle is correspondingly simple.

I have pointed out above how complex the life-cycles of Foettingeriidae become as they take to parasitism owing to the necessity of adapting themselves to successive stages in the

[1] *Paramecium* has been shown to anchor itself by means of its trichocysts (Saunders [19]). Chatton and Lwoff [3] bring forward some evidence from their silver preparations to show that trichocysts of Apostomea develop in connexion with granules formed by division of the basal granules of the cilia. It would be interesting to know how the special thigmotactic cilia develop and whether there is any connexion with trichocysts.

life-cycle of their hosts. As an example of simplification, could any organism have a simpler life-cycle than *Entamoeba gingivalis*, the amoeba of the human mouth? Its immediate environment is the *Leptothrix* colonies forming the tartar round the teeth [17]. This plant growing in the saliva evidently forms a suitably uniform environment. The amoebae, if left undisturbed, multiply prodigiously by simple fission, burrowing among the *Leptothrix* threads, especially on the lower side of the tartar towards the gingival space. Here they find for food quantities of salivary corpuscles, as well as bacteria and other organisms or debris. This is apparently the complete life-cycle: no sexual process has been described, and no cyst, infection being easily transmitted by contact. *E. gingivalis* is not strictly specific to man, being also common in the mouth of cats and dogs where the tartar environment is similar.

Host-Parasite Relationships: Specificity

It seems strange that the two new Thigmotricha briefly described above appear each to be restricted to one of several piddocks burrowing closely together in the muddy sand. The three specimens of *Petricola pholadiformis* examined were all infected with *Sphenophrya*. In another collection from the same region at Whitstable there were unfortunately none of this host, but about a dozen of its mimic *Barnea* (*Pholas*) *candida* L. These were found to be consistently free of the parasite, and so also were several specimens of another piddock, *Pholas dactylus*. The latter had, however, very heavy infections of the Ancistrid (Fig. 7), which has not been recorded before, so far as I can discover. Since the active forms of these two ciliates appear to be able to live freely for some time in sea-water, one would expect specimens which have escaped from the mollusc to be drawn into the mantle cavities of any other bivalves in the neighbourhood. It is evidently by no means in all that they can establish themselves, and possible explanations of such specificity (that is, the restriction of a parasite to a single species of host) will be referred to below. Similar problems, of course, arise in connexion with the epizoic fauna of other marine and freshwater animals. The freshwater shrimp *Gammarus pulex*, for instance, has growing on it, as a rule, numerous different Infusoria. Much has been written about the specificity

of these associations. If it were true, as Fauré-Fremiet [7] concluded from his experiments, that all the infusorian asks of its host is support and movement, then indeed it would be difficult to understand why *Opercularia*, for instance, from *Gammarus* should not live equally well on other crustaceans. Such epizoic forms would be merely passengers, not commensals or parasites, and might presumably live happily on a glass slide kept moving in the water.

However, it seems much more likely that the chief requirement of each epizoic commensal is to be carried by its host to regions where suitable food is plentiful. This implies, of course, also that the water should have and maintain a suitable pH. There is little doubt that epizoic Infusoria are more susceptible to changes in pH, and much more particular as to their food, than are their hosts.

Lady Muriel Percy has in this department studied for some years the epizoic vorticellids on *G. pulex* collected from various parts of England. She tells me (unpublished communication) that *Zoothamnium* was found to thrive best on a small bacillus (not unlike *B. coli* in appearance) which grows prodigiously in cultures of decaying elm leaves—a favourite food of *Gammarus*. In localities where there is no such food, *Zoothamnium* is absent or occurs in small numbers only.

Further, it is an interesting ecological fact that where there are enormous colonies of these vorticellids, there the suctorian *Urnula* may be found preying on them. It seems well established that all three of the vorticellids, *Zoothamnium*, *Epistylis*, and *Carchesium*, are attacked by the same species, namely *U. epistylidis* (Fig. 8), found growing also on *Dendrosoma* by Hickson and Wadsworth [12]. The latter said they were not satisfied as to the food of *Urnula*. Lady Muriel has studied the whole life-cycle, including the feeding habits, and observed the sucking dry of a succession of host zooids. There can be no doubt that *Urnula* is a parasite, perhaps the only epizoic protozoon on *Gammarus* that can be definitely incriminated, though it preys, not on the shrimp itself, but on its commensal vorticellids.

I have mentioned above as they occurred any Protozoa which appear to be specific to a single host: they are very few, the two freshwater Foettingeriidae and possibly a few Thigmo-

tricha. It may perhaps be of some interest to consider for a moment what truth there is in the statement often made, that strict specificity is shown by gregarines. Here, of course, we are dealing with true endoparasites absorbing by osmosis the host's body fluids or digested food. All have succeeded in establishing themselves so well that they are tolerated, i.e. produce no

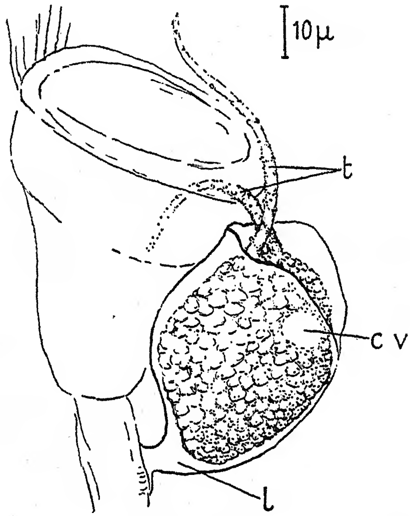

FIG. 8. *Urnula epistylidis* fixed to stalk of *Zoothamnium* (outlined). *cv*, contractile vacuole; *l*, lorica; *t*, tentacles, one inserted into the gullet of host. (After Percy.)

symptoms of disease in the host, which easily repairs any slight injury inflicted. Since gregarines are characteristically capable of reproducing in enormous numbers, tolerance can only be explained as due to a balance having been established between their reproductive powers and the resistance of the host. It is obvious that such a state cannot be permanent—sooner or later the balance must be upset, perhaps owing to some change in external conditions, and either host or parasite will gain the upper hand. Tolerance, then, is only a stage between disease and immunity.

Following the vegetative stage in gregarines there is the characteristic sexual stage, here an integral part of multiplica-

tion (so different from its seemingly fortuitous occurrence in the life-cycle of Foettingeriidae). In gregarines living in the alimentary canal, as soon as a pair has associated and encysted all subsequent stages leading to spore production may take place *in vitro* and so be followed under the microscope. No one has, however, yet induced the spores to open *in vitro*, and the young gregarines to go through their trophic stages in artificial culture. Many gregarinulae, as they escape from their spores in the alimentary canal, pass through its wall into the coelom or its chambers, such as the sperm sacs of earthworms, and there go through all stages, sexual as well as vegetative. These, known as coelomic gregarines, are typically monocystid. In the well-known genus *Monocystis* itself the host-parasite relations are very diverse—some species, for instance, *M. lumbrici* and *M. agilis*, may attack earthworms of different species or even different genera; whereas a few, such as *M. hirsuta* and *M. magna*, are each restricted to a single species of host (Hesse [11]).

In other groups of gregarines, however, we find more definite examples of specificity, and I may here mention three which seem of some general interest.

1. The total absence of coelomic gregarines from *Arenicola grubei* and the constant presence of *Gonospora arenicolae* in *A. ecaudata*, when both these species of *Arenicola* live together in the sand under identical conditions, for example, on Drake's Island at Plymouth. This, as we suggested in 1919, might be explained as due to *A. grubei* having passed through a stage of tolerance to the parasite and become immune. It is almost inconceivable that spores, which must be scattered in the neighbourhood, should not be ingested by both worms. If, however, individuals of one species developed the power of preventing ingested spores from opening or in any other way resisting infection, it would be at an advantage. Even so slight an advantage as not being infected with gregarines would tend to allow such hosts to survive in the struggle for existence, and in course of time immunity could thus have been established.[1]

[1] It is interesting to find that in nature nearly all macaque monkeys are infected with the flagellate *Trichomonas*. Dobell [5] concludes from some of his numerous experiments in which he failed to infect them artificially that any found uninfected were already immune or uninfectible. As *Trichomonas* appears to be harmless there is probably only an incredibly slight advantage derived from immunity, which would account for it not having already swept the macaque population.

2. We have examples of remarkably persistent infection where a single species of gregarine has accompanied its host over wide geographical areas. *Urospora chiridotae*, for instance, is to be found in the sea-cucumber, *Chiridota laevis*, in Russia, Greenland, and New Brunswick [15]. We cannot imagine that these infections could have started separately at such distances apart and may therefore assume that the *Chiridota* was infected a long time ago before it became so widely distributed.

3. An intestinal gregarine of some interest from the host-parasite point of view and with a wide geographical distribution is *Nina*. It was noticed in 1932 that the *Nina* found in Bermuda in the centipede *Scolopendra subspinipes* appeared to be identical with that described by Léger and Duboscq [6] from the large Mediterranean centipede *S. cingulata*. Unfortunately in the interval, a similar parasite preserved in a single specimen of *S. subspinipes* in the Moluccas had been endowed with another name: it was not till 1936 when in Malaya that I could identify this with the Bermudan *Nina* from the same host, by studying numerous living specimens at all stages. On my return, Professor Duboscq very kindly sent me from Banyuls some centipedes infected with the *Nina* he had described. These lived in my laboratory for months. I was thus able to compare, stage by stage, the long and interesting cycle, including the special contrivance for the dispersal of the spores of this gregarine, with that of the Bermudan and Malayan specimens. In this way, I satisfied myself that the *Nina* from these three localities have no constant morphological differences and are, in fact, one and the same species [16].

On looking up the distribution of the *Scolopendra*, it was interesting to find that *S. subspinipes* and *S. cingulata* are considered to be closely related species. There is some evidence, therefore, that we have in this *Nina* a parasite which is phylogenetically older than at least one of its hosts. In other words, that the common ancestor of these two centipedes was already infected by this species of gregarine (see also p. 265).

There is little doubt that the best practical[1] way of attacking

[1] It is surprising how easily some invertebrates can be infected, if infectible. The centipedes would readily feed on Horlick's malted milk, by which means spores of *Nina* were easily introduced and heavy infections obtained. This food, so easily sterilized, may be useful in rearing clean specimens of other hosts.

these specificity problems is by trying to infect clean-bred hosts with a single species only. Thus Bishop [1] has shown, by infecting clean tadpoles, that the common *Trichomonas* from frogs and toads is one true species, *T. batrachorum*, which can also infect larval salamanders.

In conclusion, it seems possible, on the one hand, that loss of specificity may occasionally have been caused by the parasite remaining unchanged morphologically while the host has become differentiated into two species. On the other hand, certain parasites may have become specific to a single host owing to its neighbours having become immune to them.

These suggestions are submitted as possible explanations of the perplexingly diverse host-parasite relations to be found among parasitic protozoa, especially such old-established parasites as the gregarines.

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HELMINTHS AND EVOLUTION

By H. A. BAYLIS

THE study of parasitic worms raises several interesting and difficult evolutionary problems. Firstly there is the question of the origin of the helminths themselves, and, necessarily bound up with this, the origin of their mode of life. The consideration of these questions leads naturally to the problem of the adaptation of particular parasites to particular hosts, and this again to the question what light, if any, the present host-distribution of the parasites may throw upon their own evolutionary history or upon that of their hosts.

The origin of helminths

It must be confessed at once that very little is known, or can be conjectured with any degree of probability, concerning the phylogenetic origin of any of the groups of helminths. The difficulty is increased by the fact that two of them (the Cestodes and the Acanthocephala) are entirely endoparasitic, having no free-living representatives and passing no stage of their life-cycle, apart from the egg,[1] outside an animal host. Most Trematodes and many parasitic Nematodes, however, do exhibit at least one larval stage capable of existing, for a time, as a free-living organism.

The free larval stages of the ectoparasitic Trematodes (Monogenea) commonly resemble their parents, and throw little more light on their probable ancestry than is to be obtained from a study of the morphology of the adults. In the endoparasitic Trematodes (Digenea), whose life-cycle is indirect and complicated by an alternation of hosts, the first (and sometimes the only) free-living stage is the miracidium, a simply-organized ciliated larva which serves for the infection of the first host (almost invariably a mollusc). There is usually a second free stage, the cercaria, which is the product of the first or asexual reproductive cycle, and serves, directly or

[1] The coracidium of Pseudophyllidean Cestodes may be regarded as a ciliated, free-swimming egg.

indirectly, for the infection of the host in which the sexual cycle takes place. The morphology of the cercaria may throw interesting light on the relationships of adult Digenea *inter se*, but affords little help in attempting to correlate them with other groups.

The Nematoda, whatever their origin may have been, form to-day one of the most widespread, numerous, and successful classes of the animal kingdom. Representatives of the group have become adapted to almost every kind of environment in which animal life is possible. Though it is still commonly stated, chiefly by the writers of general zoological text-books, that the Nematodes are mainly parasitic, this is entirely a misconception. It is probably true to say that the free-living genera and species at least equal, if they do not greatly exceed, the parasitic in number. The chief reason why the parasitic forms are better known to general zoologists than the free-living is probably that they are, for the most part, of much larger size and therefore easier to study. This fact is in itself a striking indication of the success achieved by members of the group that have taken to a parasitic existence.

It will probably hardly be disputed by any one nowadays that, whatever their ultimate ancestry, all the parasitic worms must have been derived from free-living forms. It is not difficult to find homologies in the structure of the different groups of Platyhelminthes (especially the mainly free-living Turbellaria and the parasitic Trematoda and Cestoda) that suggest that they all had a common origin. Leuckart [17] argued, in a general way, in favour of the derivation of the Trematodes from the 'Planarians' (i.e. Turbellaria), and considered that the Cestodes originated directly from the Trematodes. The Cestodes, he says,[1] 'represent in a certain sense Trematodes without an intestine, in which the organism has, according to the law of alternation of generations, separated itself into two genetically combined individual forms'. Leuckart is apparently referring here to the 'head' or scolex, which occurs in the larval stage, and the sexually mature segments or proglottids which are added to it in the adult, and which he regarded as a chain of individuals.

Little further light has been shed upon the origin of these

[1] *The Parasites of Man*, English translation by W. E. Hoyle (1886).

groups since Leuckart's day, but zoologists have become somewhat more cautious in attempting to derive one existing group directly from another. Stunkard [25], for example, considers that all the Platyhelminthes, together with the Mesozoa, may have been derived from 'planula-like' ancestral forms. Fuhrmann [10, 11], however, following Meixner, still looks upon the Monogenea, Digenea, and Cestoda as having all evolved directly and independently from Rhabdocoele Turbellaria, thus placing the Cestode branch only a degree nearer to the root of the phylogenetic tree than did Leuckart. The ancestors of the Monogenea, in his view, were probably parasitic Rhabdocoeles which, like the Temnocephalidea, were provided with a posterior sucker-like organ such as exists in some Rhabdocoeles (Macrostomidae) to-day. He rejects the view of some authors (Lönnberg, Wilhelmi) that the Digenea originated from the already highly-specialized Tricladida, and while he considers the Temnocephalidea 'eine interessante Übergangsgruppe' between the Digenea and the Rhabdocoelida, he does not go so far as to suggest, as Baer [2] does, that the Temnocephalidea lie in the direct line of descent of both the Monogenea and the Digenea from the Rhabdocoelida.

At what point the Cestodes branched off from the ancestral Platyhelminth stock remains very doubtful. It seems certain that they are a very ancient group, for not only are they clearly more deeply committed to a parasitic existence than any of the other classes under discussion, except the Acanthocephala, but they show an unusually high degree of 'specificity' in their adaptation to particular hosts. They have lost all connexion with the outer world except in the egg stage, and all traces of an alimentary canal, their only method of feeding being by percutaneous absorption. They thus show evidence, in a considerable degree, of the 'degeneration' which is commonly said to be a result of parasitic life.

Fuhrmann derives the Cestodes from the Anoplodiidae, a family of Rhabdocoeles parasitic in the body-cavity of Holothurians or in the gut of Crinoids, Echinoids, and Sipunculids. He regards the Tetraphyllidea as the most primitive group of Cestodes, and thinks it probable that they gave origin, through the Tetrarhynchidea, to the Pseudophyllidea, and through the Proteocephalidae to the Cyclophyllidea. This view is based

not only on morphological evidence, but on the host-distribution of the different groups, and will be further discussed in the latter connexion. The monozoic Cestodes, or Cestodaria, consisting of the Amphilinidea, with five genera, all inhabiting the body-cavity of Ganoid and Teleostean fishes, and the Gyrocotylidea, with two genera found only in the gut of *Chimaera*, are considered an isolated and aberrant group, no evidence being available as to their relationships to the rest of the Cestodes.

The Acanthocephala, like the Cestodes, lack an alimentary canal and feed by absorption, and are likewise entirely parasitic. Their ancestry is completely obscure. Although they are still generally classed with the Nematoda and Nematomorpha (Gordiacea) in a phylum Nemathelminthes, there is, in reality, little to suggest that they have any but the remotest relationship to either of these groups, or indeed that the phylum Nemathelminthes is a natural assemblage. Baer [3] thinks that the absence of Acanthocephala as parasites of Elasmobranchs suggests their terrestrial or freshwater origin.

Concerning the origin of the Nematodes it is impossible to say anything with certainty. Palaeontology and embryology give no assistance in solving the problem, while comparative morphology yields only unsatisfactory speculations. The writer [4], after reviewing these, concluded that the most plausible suggestion was that first made by Bütschli in 1876, and supported by several subsequent authors, that the structure of the Nematodes shows some resemblance to that of the Arthropoda, and especially of the insects. Of these they seem to approach most nearly to the larvae of some of the Diptera. It is just possible that at a very remote period the Nematodes may have had a common ancestry with the Arthropoda, but it would be unwise to press this suggestion, for we do not know whether Dipterous larvae show a genuinely primitive condition or are merely secondarily adapted to a special mode of life, and therefore in reality highly specialized.

The Nematodes, as we find them to-day, are a remarkably homogeneous group, and it is noticeable that the parasitic forms, in comparison with their free-living relatives, show very little of the 'degeneration' which has already been mentioned. Apart from the loss of 'eyes', and the loss or reduction of tactile

bristles and some other sense-organs, which would be of little or no use to internal parasites, and which are not present in all the free-living forms, there are few parasitic Nematodes that depart greatly in structure from what we must regard as the generalized type. Such differences from this type as they do almost universally show are in the direction of increased complexity of the genital organs and an increased rate of reproduction. These must be looked upon as special adaptations to a parasitic mode of life, and illustrate a general tendency among internal parasites to compensate for the necessarily high rate of mortality in the early larval stages.

The origin of parasitism in helminths

As has already been remarked, the Cestodes and Acanthocephala have no free-living representatives. In considering the origin of the parasitic habit, therefore, speculation concerning these groups seems of little value, and our attention must be concentrated upon the Trematodes and Nematodes.

The former group includes many forms whose connexion with their hosts is a comparatively loose one. In other groups of animals it is often difficult to draw a hard-and-fast line between commensalism and parasitism, and among the ectoparasitic Trematodes such a distinction is, in many cases, impossible. The majority of the species attach themselves to the skin or gills of their hosts, which are principally fishes, and there is often no evidence that they feed on anything but the host's mucous secretion or on epithelial and other debris. It must be assumed, however, that they derive some advantage, the nature of which is not always obvious, from their association with their hosts. Since they are, with very rare exceptions, unknown as parasites of mammals and birds, the origin of the group was probably marine. Moreover, the high degree of specificity shown by them suggests that the group is of great antiquity. The probability of this view is, as Baer [3] points out, enhanced by the fact that the hosts of the freshwater species are found mainly among the Cyprinoids, which are a very ancient group of fishes.

The species of the genus *Polystoma* occurring in Amphibia are of special interest. In these the larvae attach themselves to the gills of the tadpoles, migrating to the alimentary canal when

the gills are resorbed, and ultimately to the urinary bladder, where they become adult. This remarkable habit suggests how, in some cases, an endoparasitic mode of life may have been derived from an ectoparasitic one, but it cannot be taken as evidence that the truly endoparasitic Digenea originated directly from the Monogenea. This is, in fact, highly improbable. Since a molluscan host appears to be essential to the development of almost all Digenea,[1] it is far more likely that their ancestral forms were miracidium-like organisms which were at first free-living and later acquired the habit of associating with, and ultimately of penetrating into, molluscs.

The genera of adult digenetic Trematodes are, as Baer [3] has shown, fairly evenly distributed among the different groups of vertebrates, the largest numbers occurring in bony fishes and in birds. Extremely few are known in Elasmobranchs, and these belong to a family mainly found in migratory Teleosts (Salmonidae). These facts, together with the relatively low degree of specificity shown by the Digenea, suggest that the group is of more recent origin than the Monogenea. Studies on the structure of the adults, as compared with that of the cercariae, have led many authorities to consider the Digenea a polyphyletic group, in which convergent evolution has led to similar modifications (e.g. the disappearance of the acetabulum, or posterior sucker) in families of different descent.

It is not difficult to imagine how a free-living organism, such as we must suppose the ancestors of the Monogenea and Digenea to have been, may have begun to assume the habit of parasitism. We may suppose that some of these hypothetical ancestors first formed comparatively innocent associations with other animals, in which they played the part of commensals, or perhaps were merely carried about from one food-supply to another. The first step leading from this to a closer association may have been a change in feeding-habits. If, for example, we imagine a Turbellarian-like organism creeping about on the exterior of some larger aquatic animal, and at first acting as a scavenger and feeding on particles of organic matter, perhaps derived from the larger animal's food, we may easily visualize a gradual specialization whereby its diet becomes restricted to food of a particular kind. The ingestion, perhaps

[1] At least one species has been found to develop in an annelid worm.

accidental at first, of mucus and dead epithelial cells derived from the 'host' may become a fixed habit, and may be followed, in the course of generations, by a physiological change in the digestive organs, so that other food is less readily assimilated.

The gill-chambers of fishes, in which many of the Monogenea and some Digenea live, not only provide an abundance of mucus, in which particles of waste organic matter are included, but are in communication with the anterior part of the alimentary canal, so that it would be but a short step for the 'guest' to pass by this route from the exterior to the interior of its host. Having once taken this step, it would find new sources of food available to it, in the form of partially-digested material and also of bacteria and other organisms already inhabiting the alimentary canal. These might lead to new changes of habit, and these again to further physiological changes, and the animal would thus become more and more deeply committed to the mode of life which we are accustomed to call parasitism.

It is remarkable that, apart from the species of *Polystoma* to which reference has already been made, there is little or no evidence that such a course as this has actually been followed by any of the Monogenea. A possible explanation of this may be that their oxygen-requirements have prevented them from becoming true internal parasites. Other groups of helminths, which have become fully adapted to intestinal conditions, appear to be able to live almost anaerobically, or perhaps in some cases, especially when they ingest the host's blood, are able to derive a sufficient supply of oxygen from their food. It may be, on the other hand, that, as the hosts of all Monogenea are aquatic, there has been no danger of desiccation to drive the parasites to seek the security of an internal habitat. This danger has very probably played some part in bringing about the endoparasitic habits of the Digenea and Nematoda.

Members of the latter group with habits comparable with those of the Monogenea are not unknown. Some Rhabditidae attach themselves temporarily to insects, which they appear to use merely as means of transport. Species of free-living genera are occasionally found in the mucus on the skin of fishes, while at least one species of *Capillaria* (otherwise a truly endoparasitic genus) appears to occur in the external mucus or

epithelium of Elasmobranchs. A curious case of commensalism is that of *Odontobius*, a small Nematode belonging to the free-living family Oncholaimidae, which lives in colonies, together with certain Protozoa and other micro-organisms, in the mucus on the baleen-plates of whales.

The most simply organized and probably most primitive parasitic Nematodes belong to the family Rhabditidae, which contains also many free-living genera and species.[1] The latter are saprozoic, feeding on decaying organic substances or on the bacteria living in them. The parasitic representatives of this family, some of which have alternating parasitic and free-living generations, and those of the closely related family Oxyuridae, which contains no free-living forms, are found either in the caecum and rectum of vertebrate hosts or in the gut of invertebrates, especially insects. Here they find food of a kind very similar to that of their free-living relatives, and, granted that their eggs or larvae are able to withstand for a short time the action of the digestive juices of the host, their entry into the new environment would present little difficulty. Among the Nematodes parasitic in vertebrates, however, it is only in certain families which may be considered relatively primitive (Oxyuridae, Heterakidae) that so simple a method of initiation to parasitism occurs. So varied are the modes of entry into their hosts among other families that the conclusion seems inevitable that the habit of parasitism must have arisen independently in several distinct stocks.

In members of several unrelated groups (e.g. *Ascaris*, *Strongyloides*, and the hookworms) we find a complex larval migration taking place in the body of the host before the worms finally settle down in the intestine to become mature. This migration involves entry into the blood-stream, the larvae being then carried by the portal system to the liver, and thence by way of the heart and pulmonary arteries to the lungs. Here they ultimately rupture the capillaries and escape into the alveoli, whence they are carried up the bronchi and trachea to the mouth, are swallowed, and eventually reach their definitive location. It has been suggested that this route of migration

[1] It is of interest, in this connexion, to note that the free-living first-stage larvae of some of the more specialized parasitic forms (Strongyloidea) closely resemble the Rhabditidae in structure and habits.

represents an ancestral habit, the parasites having formerly had their habitat in the lungs, where they found an abundant supply of oxygen, and that the larvae are still unable to develop without this passage through the lungs. Experiments have shown, however, that hookworms can develop directly in the intestine, while Fülleborn has found that the route of migration followed by the skin-penetrating larvae of *Rhabdias bufonis* (a parasite of the lungs of frogs, closely related to *Strongyloides*) is the same as that followed by small inert particles subcutaneously injected, and is thus mainly due to mechanical causes. In any case, the fact that this migration takes place in genera belonging to different orders, and not in other genera of the same orders, indicates that it is not a survival of the habit of a common ancestral form, but rather a habit that has been developed independently by unrelated genera as an adaptation to similar circumstances. Its significance may possibly lie in the protection of the larvae, on their first introduction into the host, from the destructive properties of its digestive juices. There are, of course, adult forms which inhabit the blood-vessels or the lungs, and which reach them by a similar migratory process, but these throw no light on the ancestry of the intestinal parasites under discussion.

So far we have been considering forms of which the life-cycle is direct and involves only a single host. The case of Nematodes with an indirect life-cycle, involving one or more changes of host, and that of the digenetic Trematodes, where these conditions invariably obtain, present problems of much greater complexity. It is extremely difficult to explain how the alternation of hosts among the Digenea arose. Were any cases known in which, after the parasitic phase of asexual multiplication, the organisms became sexually mature in a free-living state, the problem might be easier of solution. Unfortunately, however, no instance of a free-living adult Trematode is on record.[1] Leuckart envisaged only two possible hypotheses. 'The intermediate hosts', he says, 'have either been interpolated subse-

[1] A close approach to this appears to be made by the metacercariae of some Hemiuridae, which may escape from their second intermediate hosts (Copepods) when these die, and may thus occur free in the sea, and which may already have developed functional sexual organs. It would probably make no difference to their subsequent development in plankton-eating fishes whether these metacercariae were swallowed with the hosts or separately.

quently into the life-history of the parasites, or they were originally true definitive carriers, which formerly brought their intestinal worms to sexual maturity,[1] but have since become merely intermediate, because the history of development of the inmates has extended itself over a greater number of stages by means of further formation and differentiation.' He declared himself unequivocally in favour of the latter theory,[2] which he held to apply not only to the Digenea but to the Cestodes, on the ground that the sexually mature stages of entozoa are mainly found in vertebrates, and these are of relatively recent origin. He went on to argue that the sporocysts and rediae of the Digenea were to be regarded as ancestral forms, probably derived from ectoparasitic Trematodes, and suggested that their mode of reproduction might originally have been sexual. The cercaria, he thought, originally attained maturity in a second host, and had degenerated into a mere intermediate form, so that the original definitive host had become a second intermediate host.

A third possibility, however, seems worthy of consideration. The cercarial stage may represent a form which was at one time capable, at least in some cases, of becoming sexually mature without entering a second host. We know that some Digenea (Fasciolidae, Paramphistomidae, blood-flukes) do not

[1] It is interesting to note that the hosts of one subfamily of parasitic Rhabdocoela (Graffillinae) are molluscs.

[2] Some reference to the question of the germ-cell cycle in Digenea is perhaps called for in this connexion. A useful summary of the various views that have been held is given by Cable [7], whose own studies led him to support the view of Leuckart that molluscs were the original definitive hosts. If, as the observations of Cable and most other recent authors suggest, there is a continuous lineage of the germ-cells throughout the stages, with or without polyembryony, and only one 'adult' stage in which sexual reproduction occurs, there would seem to be no difficulty in the development of this adult form being delayed until after the parasite has left its first host. But in the Gasterostomata (Bucephalidae) and in *Leucochloridium*, according to Woodhead's [27, 28] somewhat unconvincingly described observations, the sporocyst and redia are also 'adults', and reproduction in them is sexual. If these observations were confirmed, and especially if similar phenomena were found to be of general occurrence, our ideas as to the alternation of hosts might require revision. All Digenea, however, as Cable remarks, may not have the same type of germ-cell cycle. Anomalies in the succession of stages are not unknown. Sewell [23], for instance, has described a sporocyst producing, instead of rediae, a second generation of miracidia. Suppression of the redia stage is not uncommon, cercariae being produced directly by the sporocyst, while in some cases (Cyclocoelidae, *Parorchis* among the Echinostomatidae) a single redia is already formed within the miracidium before this leaves the egg-shell.

require a second intermediate host, and the supposition that all stages in the life-history, including the hypothetical sexually mature cercaria, were formerly parasitic seems unnecessary. On the contrary, the universal occurrence of a cercarial stage, having almost always at least a vestige of a tail, and the great diversity in the modes of infection of the final hosts, strongly suggest that there was originally a free-swimming sexual form.

There is evidence that, where the free-swimming cercarial stage has been suppressed, this is a comparatively recent development. Some cercariae which become encysted in the first host possess not only a functional tail but also penetration-glands and a stylet—organs characteristic of cercariae which penetrate actively into a second host. The tail is thrown off at the time of encystment, as in forms which make use of it for swimming. The cercaria of one species of *Notocotylus*, which becomes encysted in the tissues of the first host, and possesses no eye-spots and only a vestigial tail, differs in these respects from all the other known cercariae of its family, among which encystment in the open is the rule.

So great is the variety of types of life-history among the Digenea that only a few examples can be mentioned. The cercariae of some (Fasciolidae, Notocotylidae, Paramphistomidae), on leaving the first host, become encysted in the open, and are unable to develop further unless ingested by a suitable final host. Others (Echinostomatidae, Lepodermatidae (Plagiorchidae)), after leaving the snail host, enter either another snail (of the same or a different species) or some other invertebrate, such as an insect-larva, and there become encysted. In a number of cases the cercariae, without leaving the first host at all, become encysted within the redia or sporocyst. Some species may be transmitted passively to a second and even a third intermediate host. The cercariae of some families (e.g. Opisthorchidae, Heterophyidae, Strigeidae) penetrate the skin of fishes or amphibians and become encysted in their tissues, to await the ingestion of these second intermediate hosts by the final host. Among the blood-flukes the cercariae, after leaving the molluscan host, directly attack the final host (a fish, bird, or mammal), penetrate its skin and migrate into its circulatory system. It seems probable that all these types of life-cycle have arisen, either independently or as modifications

one of another, as the result of evolutionary processes, and it may well be that the connecting-link—a free-living adult form resembling a cercaria—has been lost.

In some life-cycles changes may still be taking place. Within a single genus (*Maritrema*) at least three types of life-cycle occur (Rothschild [21]). In some species the cercariae shed their tails and become encysted without leaving the sporocyst in the first host; in others they have a free-swimming stage and become encysted in a second intermediate host; while in one species two forms of cercaria develop in the same sporocyst, one leaving the host and the other becoming encysted *in situ*.

Turning to the Nematodes with indirect life-cycles, we find that the intermediate host—usually an Arthropod—almost invariably acquires infection by ingesting the larvae while they are still enclosed in the egg-shell. It is possible to regard the subsequent transference of the parasites to vertebrate hosts as an elaboration of the direct type of life-history, which may have arisen fortuitously. If an insect or crustacean infested with a primitive and adaptable kind of Nematode parasite were eaten by a vertebrate, the parasite might sometimes have been able to withstand the sudden change of environment and continue its existence in the new 'host'. Such a simple method of transference from one host to another is, it is true, unknown among existing Nematodes. As a rule the larvae of the Spiruridae and related families, after hatching, at once leave the alimentary canal of the intermediate host and enter its body-cavity or connective tissue, where a capsule or cyst is usually formed round them at the expense of the host. The first of the four moults is usually undergone before the formation of the capsule, and the second after it, so that at the time of transference to the definitive host the larva is already in the third stage. The process of encapsulement among the tissues is sometimes repeated if the first host is devoured by a vertebrate which is not the normal definitive host.

Though we have at present no means of tracing the steps by which such life-cycles as these have reached their present degree of complexity, it must be supposed that they are the result of adaptive evolutionary processes. Even more difficult to explain is the origin of the life-cycle of the Filariidae, where there is an alternation of hosts between a vertebrate and a

blood-sucking insect, with the most delicate adjustments between the habits of the parasite and those of its vector.

Specificity and host-distribution in relation to evolution

The more or less strict confinement of parasitic organisms to particular hosts is generally known as specificity. Among helminths instances of every degree of this are to be found. Parasites may be designated polyxenous, oligoxenous, or monoxenous (Sandground [22]), according to whether they are capable of establishing themselves in many kinds of host, in a restricted number of kinds, or only in a single kind.

A striking example of strict specificity is furnished by the Temnocephalidea, now generally considered to be a highly specialized group of ectoparasitic Turbellaria. This group, containing only 28 known species, is divided by Baer [2] into no less than eight genera (seven of which consist of single species) and four families. One family contains three monotypic genera, all confined to Decapod Crustacea of the family Atyidae. Two other families, each containing a single genus and species, are confined to the Parastacidae. The family Temnocephalidae (*s.s.*) consists of three genera, two of which are monotypic and occur on Decapods, while the third (*Temnocephala*) has 21 species, of which 18 occur on Decapods, one on an Isopod, one in the mantle-cavity of a Gastropod, and one on freshwater tortoises.

In such a case as this we can, in imagination, follow the process of evolution. One can visualize an originally plastic and adaptable stock giving rise to races which became isolated by association with hosts of different kinds, and became more and more highly specialized. This specialization, at first probably physiological, was evidently accompanied by increasing morphological differentiation, leading to a splitting-up of the original stock into branches which were at first of the order recognized by systematists as specific, and later became so far removed from each other as to justify the formation of generic and finally family concepts.

That such an imaginary picture of the course of events is not a mere begging of the question seems clear from the manner in which it is borne out by innumerable examples throughout the field of helminthology. Baer [3] has made an interesting

analysis of the extent to which specificity is shown by different groups of helminths. He finds that the ectoparasitic Monogenea are much more strictly specific than the endoparasitic Digenea. Among them the genera *Nitzschia* and *Diclibothrium* occur only on sturgeons, several genera only on Elasmobranchs, *Discocotyle* only on Salmonidae, *Dactylogyrus*[1] only on Cyprinidae, and so on, whereas among the Digenea it is not uncommon to find a single species capable of living in hosts belonging to widely different groups.

Among the Cestodes, the adult forms of the Tetraphyllidea (excluding the families Monticelliidae and Proteocephalidae) are peculiar to Elasmobranchs, and do not occur in bony fishes. The Tetrarhynchidea occur in Elasmobranchs and Ganoids, the Monticelliidae in Siluroids, and the Proteocephalidae in freshwater fishes, amphibians, and reptiles. Fuhrmann, as we have seen, considers the Tetraphyllidea a primitive group, possibly representing the ancestral stock from which the other groups originated. With the gradual extension of their host-range to the higher groups of vertebrates some of them became modified, according to his theory, into forms like the Tetrarhynchidea and the Proteocephalidae, and these again into forms like the Pseudophyllidea and Cyclophyllidea respectively, these last two groups now occurring in all classes of vertebrates.

The great majority of the genera of Cyclophyllidea occur in birds, and are represented by forms showing a marked degree of specificity. Baer points out that the birds seem to have evolved very suddenly and rapidly, and that this 'explosive' evolution is probably reflected in their Cestode parasites. The evolution of the mammals, on the other hand, seems to have been slow and gradual, and here we find a comparatively small number of Cestode genera, the same genus (though not the same species) frequently occurring in several orders.

Some account of the host-distribution of the Nematodes of vertebrates has been given by the writer [5]. It is shown that, broadly speaking, the forms with a direct life-cycle show a greater

[1] Bychowsky [6] concludes from his observations on *Dactylogyrus* that its species 'are parasitic only on a single host-species, or on several closely-related species belonging to one and the same genus, or on species which, even if belonging to different genera, are capable of producing hybrids'.

degree of specificity than those with an indirect life-cycle. As a tentative explanation of this fact, it is pointed out that the larvae of the former are usually at a younger and less resistant stage of development at the time of penetration into the definitive host, and therefore probably less tolerant of hosts to which they are imperfectly adapted. Forms with an indirect life-history generally show a stricter specificity for their intermediate than for their definitive hosts, and this may be explicable on similar lines.[1]

Baer, in analysing the distribution of the genera of Nematodes among the orders of vertebrates, finds that their numbers form an ascending scale from the Elasmobranchs to the mammals. The significance of this fact is not altogether clear, but while it suggests that the Nematodes did not, to any great extent, become parasitic in vertebrates until the latter had taken to a terrestrial existence, it also seems to indicate that the parasites, by parallel evolution, became more highly specialized *pari passu* with their hosts.

Most of those who have studied the phenomenon of specificity are agreed that it is the result of gradual evolutionary processes, and it is generally, and not unreasonably, assumed that a high degree of specificity indicates extreme specialization, while polyxenous parasites are to be regarded as relatively primitive. So delicate are the adjustments between parasite and host—as is clearly shown by the frequent failure of infection-experiments with unusual hosts, even though these may be closely related to the normal host—that a process of selective adaptation seems the only possible explanation of their origin. As Chandler [8] puts it, 'the segregation of adaptable races stands out as the most probable and most frequent factor involved in the formation of "hostal" races'. Such segregation, as he observes, presupposes the widespread occurrence of genetic impurity among races of helminths, as elsewhere in nature, and the instability (or variability) of their physiology and morphology. Granted the existence of these factors, adaptation to a

[1] It is curious, in this connexion, as Baer [3] remarks, that the larval stages of the Digenea are highly specific, whereas their adults show so little specificity; while, on the other hand, adult Cestodes are usually highly specific and their larvae much less so. This perhaps suggests that the adaptation of the Cestodes to their intermediate hosts was secondary—*vide* the first of Leuckart's hypotheses referred to above (p. 257.)

particular host might result from the initial selection of an adaptable race of parasites, and would probably tend to become more perfect with successive generations.

It must be remembered, however, that the successful adaptation of a parasite to its host depends largely upon the ability of the parasite to avoid producing intolerance in the host, or causing so much damage, or so violent a reaction, as to endanger either its own survival or that of the host-species. A good deal of evidence has accumulated recently to show that some resistance on the part of the host often has to be overcome by the parasite. We now know that many helminths, like bacteria and other micro-organisms, can act as antigens and cause the production of antibodies in the blood of the host, and that a light infestation with a worm parasite may confer on the host some protection against reinfection. This aspect of helminthology cannot be fully discussed here, but is mentioned because it emphasizes the point that adaptation implies the establishment and maintenance of a certain state of equilibrium between parasite and host, and in this sense may be regarded as mutual. It is not surprising, therefore, to find that many helminths, though not monoxenous, are better adapted to some hosts than to others. There may be one particular host-species in which the parasite finds conditions more suitable than in any other, and this has been defined by Sandground [22] as the 'normal' host-species.

Different races of the same original stock may in this way become adapted to different hosts. There is evidence of such adaptation among the Nematodes that attack plants (see Steiner [24]), and some evidence suggesting the existence of 'host-races' or 'physiological strains' among worms parasitic in animals—e.g. *Ascaris lumbricoides* of man and pig; *Ancylostoma caninum* of dog and cat; *Hymenolepis nana* of man and rodents; various strains of *Strongyloides*, &c. Such host-races may be looked upon as incipient species, which may eventually become morphologically distinguishable, and under the prolonged action of segregation may diverge so far as to be generically separated. As we have seen, this seems to have been the case with the Temnocephalidea.

The origin of specificity among helminths appears to offer so striking an example of the operation of natural selection that

it is curious that it should not have attracted the attention of Darwin. It was not unnoticed by Weismann [26], though he did not discuss it in detail. Weismann saw in the life-histories of parasites evidence of adaptations arising 'not through the selection of indefinite variations, but through that of variations in a definite direction', this definite direction being 'determined only by the advantage which it affords to the species with regard to its capacity for existence'.

Petrunkevitch [20] argues that the adaptation of an internal parasite to a particular host can only depend upon 'chemical' or 'assimilative' mutations originating in the germ-plasm of the parasite, as opposed to structural mutations. He is of the opinion 'that the formation of new species, in parasites at least, can not be due to natural selection of advantageous mutations and that the destructive influence of the environment is directed not toward the elimination of less fit individuals, but toward the stabilization of the existing stock'. The 'environment' here referred to is that of the interior of the host, and the argument of Petrunkevitch is clearly applicable only to the final stages in the development of strict specificity, where the stability of this environment is unquestionably of great importance. His examples are mainly drawn from genera, such as *Taenia*, which appear to be already highly specialized and highly specific, and cannot legitimately be used as arguments against the operation of natural selection, as ordinarily understood, in the earlier stages of adaptation to parasitism.

The study of host-distribution in some groups of parasites, notably the Mallophaga of birds and mammals, and certain Protozoa in frogs and termites, has been held by some authors to throw valuable light on the relationships and geographical distribution of the hosts (for references see Kirby [16].) Von Ihering [13], who based his arguments on helminths, seems to have been one of the first to apply this principle, which has been called the 'host-parasite method' or the 'von Ihering method'. The facts upon which he relied were, however, both inadequate and inaccurate. He thought, for example, that the occurrence of the Nematode *Dioctophyme renale* [*Eustrongylus gigas*] in wild Canidae in Europe and South America necessarily indicated that it had existed in their Upper Miocene ancestors. The fallacy of this argument is obvious, and in fact

the same parasite has been recorded not only from other carnivores but from the horse, ox, pig, orang-utan, and man.

Johnston [14] points out that the Trematodes of Australian frogs have their closest relatives in the frogs of Europe, America, and Asia, and uses this fact in support of the view that the frogs originated in a hypothetical Palaearctic centre in geological times.[1] Similar arguments are drawn by him from the Cestodes and Trematodes of Australian and South American marsupials, and [15] from certain Trematodes of birds (see also p. 246).

It seems, however, very doubtful how far we can rely upon the results of the 'von Ihering method' when it is applied to helminths. From a survey of a large number of the better-known genera in the four main groups of helminths, the writer is convinced that the habits (particularly as regards food) and environment of the hosts have played a far more important part in determining their helminth fauna than have their phylogenetic relationships. Representative species of the well-known Nematode genus *Oesophagostomum*, for example, have been recorded from Primates, swine, ruminants, rodents, an armadillo, and a wild cat, and several of the species apparently occur both in the wart-hog and in antelopes. The common hookworm *Necator americanus* has been found in man, various other Primates, the dog, pig, rhinoceros, a pangolin, an armadillo, and a tree-porcupine. The gapeworm genus, *Syngamus*, has representative species in birds, ruminants, carnivores, elephants, and the hippopotamus. Of the genus *Cruzia* nine species have been described, one of which occurs in opossums, one in the pig, three in armadillos, two in lizards, one in a tortoise, and one in a toad. Innumerable examples of this kind could be quoted from among the Nematodes, and many similar cases occur in the other groups. Among the Cestodes, for instance, species of *Oochoristica* occur in mammals as well as in reptiles, *Mesocestoides* occurs in birds of prey as well as in carnivorous mammals, and *Tetrabothrius* in Cetacea and seals as well as in fish-eating birds of several orders. The life-history of *Mesocestoides*, and that of the Ascarid genera *Anisakis*,

[1] Metcalf [18, 19] comes to quite different conclusions from the distribution of Opalinid Protozoa in frogs. He believes, for example, that the Leptodactylid frogs originated in South America and passed by some southern route to Australia. His views have, however, been strongly criticized by Dunn [9].

Porrocaecum, and *Contracaecum*, all of which have representatives not only in birds but in fish-eating marine mammals, explain their wide distribution, for they all have as their intermediate hosts creatures liable to be preyed upon by the various final hosts. Food and feeding-habits are not, however, always of first importance. Of the monogenetic Trematode genus *Polystoma* some twenty or more species have been recorded from freshwater tortoises, and six from Amphibia. The infection of the host in this genus does not depend upon the ingestion of the larvae, and the aquatic environment seems to have been the principal factor.[1]

If we pick out genera which are strictly confined to groups of hosts known to be closely related, we find that they are almost always highly-specialized genera whose relationships are somewhat obscure, and usually also that their hosts are likewise highly-specialized animals. Even so, with increasing knowledge, their specificity sometimes proves to be less strict than was supposed. As a classical example of specificity among the Nematodes those found in elephants are often quoted. A few years ago it was thought that there were nine genera of Strongyloid Nematodes that occurred in elephants and in no other host. Of several of these genera representative species (but never the same species) had been found in both the Asiatic and African elephants; representatives of others were known only in one of these hosts or the other. As the result, however, of further study and the description of more species, not only have the nine genera been reduced to four, but it has been found that species of all these four occur not only in both kinds of elephant but also in the African rhinoceros, while one genus also has representatives in the wart-hog.

It was formerly possible to build up a very pretty theory on the known facts. Since these genera were peculiar to elephants, and several of them had representative species in both kinds of elephant, they must have descended from common ancestors which had existed in the common ancestor of the elephants, and their subsequent evolution had proceeded parallel to that of their hosts, leading to a gradual divergence in their morphological characters. Up to a point this reasoning may still be quite sound, but, since we know that the premisses were so de-

[1] A closely-related form, *Oculotrema*, is recorded from the eyes of the hippopotamus.

fective, it has lost much of its force. We might, on the new facts, build up another theory. We might say that, since these genera occurred in other African animals besides the elephant, and were unknown in Asia except in the Indian elephant, the origin of the latter animal must have been African. But this is contrary to the palaeontological evidence, which indicates that, although the earliest known ancestors of elephants lived in Africa, the recent African elephants are derived from Asiatic forms.

The host-distribution of the Nematode genus *Crossocephalus* is rather suggestive. Of this genus at present three species are known, one occurring in zebras and two in Asiatic rhinoceroses. This distribution may just possibly be due to the rather remote phylogenetic connexion between the hosts, as may also that of the lungworm *Dictyocaulus arnfieldi*, which has been recorded from the Malayan tapir as well as from Equidae. But, like most genera with a limited host-range, these appear to be highly-specialized forms. When we consider such a genus as *Trichonema*, more than thirty species of which are found in Equidae, and none in any other host, we can only conclude that its specificity is due to long isolation. Many similar cases could be mentioned. The Acanthocephalan genus *Bolbosoma*, for instance, is peculiar to Cetacea, as are the Nematode genus *Crassicauda*, which inhabits the urino-genital system, and *Pseudalius* and several other genera inhabiting the lungs and blood-vessels. Five or six species of *Echinocephalus* occur in Elasmobranchs (chiefly sting-rays), while the very closely related genera *Gnathostoma* and *Tanqua* occur respectively in mammals and reptiles. *Kalicephalus*, another genus of Nematodes, has a large number of very similar species, occurring only in snakes. Among the Cestodes, *Andrya* appears to be confined to rodents, *Thysanosoma*, *Avitellina*, and *Stilesia* to ruminants, *Tatria* to grebes, *Gyrocoelia* and *Progynotaenia* to Charadriiform birds, and so on.

These examples all tend to show that the characters of species confined for a long period to a restricted group of hosts have eventually become so specialized that they are now regarded as generic. Host-distribution should therefore, in theory at least, yield more valuable information as to the relationships of the hosts when species and not genera of parasites form the material for study. In practice, however, it is often very difficult to interpret the facts. Many helminths seem to display

a complete disregard for so-called geographical barriers. Baer [1] considers a Cestode occurring in the South American rhea distinguishable at most subspecifically from *Houttuynia struthiocameli*[1] of the African ostrich. The same author [3] draws attention to the fact that two Cestodes found in the European freshwater eel (*Anguilla anguilla*), namely *Bothriocephalus claviceps* and *Proteocephalus macrocephalus*, appear to be identical with two found in its counterpart (*Anguilla rostrata*) of the eastern side of North America. These parasites can hardly be acquired by the larval eels in mid-Atlantic, and it is difficult to believe that this is a double case of convergent evolution. The Nematode species *Porrocaecum crocodili* has been recorded from crocodiles in West Africa, the Malay States, and Australia. Innumerable similar instances could be quoted, apart from the parasites of man and his domestic animals. There are, however, many possible means of dispersal for helminths or their eggs and larvae, and too much weight must not be given to apparent cases of discontinuous distribution.

Fuhrmann [12] believes that among the Cestodes of birds every species is strictly confined to hosts belonging to a particular order, and although there may be some exceptions to this rule (not necessarily due to accident or to faulty observation, as Fuhrmann maintains), nevertheless there is good reason for thinking that, in general, the rule holds good. In large genera representative species may occur in birds of many orders, and a single species may occur in many hosts, but it is at least exceptional to find that these hosts belong to different natural groups. The same principle is, to some extent, applicable to other groups of helminths, but in these the exceptions are more numerous and are sometimes quite startling (e.g. the case of *Necator americanus*, already mentioned). It seems, therefore, that, although the attempt to draw conclusions as to the relationships of animals from their helminth parasites may sometimes yield interesting results, it is fraught with so many pitfalls that it should only be made with the greatest caution.

This essay cannot claim to have given a satisfactory answer to any of the questions propounded in its opening paragraph. Some

[1] Baer calls the species *H. struthionis* (Houttuyn, 1773), but this name does not appear to have been used by Houttuyn, and *struthiocameli* (Rudolphi, 1810) has priority.

of the evolutionary problems of helminthology may, indeed, never be solved, but this review of the subject will be justified if it should succeed in drawing more general attention to the interest of these problems, and still more so if it should be found to suggest any lines of investigation which may lead a little nearer to their solution.

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THE DESCENT OF CRUSTACEA FROM TRILOBITES, AND THEIR LARVAL RELATIONS

By WALTER GARSTANG *and* ROBERT GURNEY

IF a case were known in which an existing class of animals with a metamorphic life-history could be traced back with absolute certainty to its origin in another class that preceded it geologically, and if the ontogenies of both classes were sufficiently well known for comparison, we should have the most complete portrayal of the course of evolution that the heart of a biologist could desire. We should see in what respects the derived ontogeny was still repeating the ancestral ontogeny, and at what points it had deviated from it. The part played by ontogeny in recapitulating the past, and in creating new departures for the future would be at last, and for the first time, unequivocally demonstrable.

With these thoughts in mind, and believing that Crustacea and Trilobites offered the best prospect of fulfilling the required conditions, the authors of the present essay have together examined the problem and made a combined attempt to realize the dream. We have convinced ourselves that the growing tendency to regard the Trilobites as primitive, and indeed ancestral, Crustacea, is well founded; and, since the outlines of their structure and development are becoming known with increasing precision year by year, the material is almost to hand for a comparative survey.

Everything, however, depends on the direct relationship of the two groups being firmly established, and zoologists have not hitherto shown any eagerness to accept it. We accordingly address ourselves in the first instance to the problem of Crustacean ancestry.

The Ancestry of Crustacea

From Claus's classical work on the Foundations of the Crustacean System we extract in abbreviated form the following passage (translated):

'Phyllopods appear to be the least changed of all the descendants, Malacostraca and Entomostraca, of the original Crustacean stock. I have accordingly distinguished the old progenitors themselves as "Urphyllopoden" (Protophyllopoda, Balfour, 1885), but without any intention of implying close agreement in details between them and modern Phyllopods. On the contrary, if fossil remains could give us a clear picture of their body-form and appendages, we should hardly recognize their Phyllopod character. In particular they would possess complete mandibular and maxillary appendages; their limbs would be neither Phyllopod nor Schizopod, but of an intermediate kind; gills on the basal segments of their legs would be missing, since such things would be the result of later elaborations, and probably their second antennae would be concerned both with locomotion and food-manipulation, at least in the earlier forms' [9, p. 100].

This reconstruction by Claus of the ancestors of Crustacea was based solely on his studies of the anatomy and development of living forms. The Cambrian fauna was then practically unknown, and only the crudest evidences of Trilobite appendages had been put forward. Various Crustacean types were known to have been contemporary with Trilobites in the so-called 'Primordial Fauna', but there was nothing as yet to mark either of them as more primitive than the other. Since then, however, new terrains have been explored, and palaeontologists have unearthed intelligible remains of equally definite, but less specialized, Trilobites as far down as the Lower Cambrian [40], while Walcott [41] has revealed the existence in the Middle Cambrian of a galaxy of strange Crustacea which display Trilobite features of one kind or another to varying degrees of completeness. Moreover, every point in Claus's forecast of the 'Urphyllopod' has been demonstrated to be characteristic of Trilobites themselves. May we not then assume that Trilobites, whether Cambrian or Pre-cambrian, were the actual progenitors of all Crustacea?

This question has been answered affirmatively and with confidence by distinguished palaeontologists and, if some of Raymond's principles of phylogenetic reconstruction [34] are open to criticism, this remark cannot be made of Beurlen's strictly objective and logical treatment, which he sums up in the conclusion that 'Trilobites . . . embody everything that theory requires of the Crustacean basal stock, and indeed in

so beautiful a manner that we can hardly expect its like in the whole animal kingdom' [2, p. 469].

Hitherto zoologists have been more inclined towards the theory of a 'common origin' of the two classes than of the derivation of one class from the other, though Calman came near it in his excellent text-book [5, p. 26]. One might, of course, bring forward Walcott's *Yohoia* and *Opabinia* from the Middle Cambrian as possible connecting links between early types of Trilobites and such Anostracan Branchiopods as *Thamnocephalus*, but in our imperfect knowledge of all three types an element of uncertainty would still remain. Walcott himself regarded the Trilobites and Limuloids as 'directly descendent' from *Apus*-like Branchiopods [41, pp. 161–5].

In the Devonian fossil *Lepidocaris*, however, so admirably worked out and restored by Scourfield [36], we at last appear to have a link so firm as to place the Trilobite theory of Crustacean origin on an almost unassailable foundation. Its numerous paired pleural 'scales' are clearly homologous with the proximal exites (pro-epipods) of Anostraca, as Scourfield, Calman [6], and Borradaile [3] have suggested, but their mode of development, by the successive 'pinching-off' of lateral folds of the body-rings, marks them even more decidedly as the exact homologues of Trilobite pleura [36, pp. 161, 176, Figs. 38, 39]. Even the terminal spines they bear, which are lacking in Anostraca, regularly recur on the pleura of almost every Trilobite. Nevertheless the proximal exites of Anostraca differ from the more distal and vesicular gills (metepipodites) in usually having a more or less denticulate edge, and, although the leaf-like form is rare (*Thamnocephalus*), there are traces of a pointed distal extremity in many genera [10]. Their broad bases of attachment to the limb, and their tendency to distal expansion and bifurcation are possibly adaptive to the valvular function which Cannon [8] claims for them in connexion with polypodial methods of food-gathering.

The transformation of a rigid pleurite of the body to a flexible epipodite of the leg is an example of a momentous evolutional change wrought by very simple means—practically nothing more than the introduction of a dorsal line of articulation. The pleurite bore the limb at its base ventrally, and, when the articulation arose, the pleurite would at once drop

over the limb as a basal or precoxal appendage. Its thin ventral wall, like that of a Mysid's carapace, doubtless functioned originally as a gill, under which the exopodite maintained a constant change of water. After the change, when it and the exopodite were drawn into the service of food-collection, gills presumably developed on the legs themselves. A passage in Professor Goodrich's illuminating book on *Living Organisms* is so appropriate that we cannot resist its quotation:

'Entirely new functions and entirely new organs are not suddenly developed. All are evolved by the gradual transformation of, addition to, or subtraction from something already there. . . . In the evolution of an organ by natural selection every stage must be useful, and it is often difficult to picture the intermediate conditions' [15, p. 141].

It is not only in its pleural scales, however, that *Lepidocaris* displays Trilobitic affinities. The scales, as articulated structures, end at the twelfth or genital somite, but their terminal spines continue in unbroken sequence backwards to the last somite, as in Lower Cambrian Mesonacids [40, Pls. 23, 26; 39, Figs. 182, 183 B]. Somites 12–15 provide intermediate stages in which the diminishing pleura are clearly seen to be somatic, not appendicular, in origin. The last or caudal somite is elongated and compound, and consists plainly of two abdominal somites fused with a short telson. Its armature is remarkable, for, as Scourfield has shown, it bears two pairs of lateral styliform articulated processes, tipped with setae, which have precisely the same relation to the pleural spines as the limbs in front to the pleural scales overhanging them, and must be interpreted accordingly as vestigial appendages. We propose to distinguish them as anterior and posterior cercopods. The posterior pair undergoes special enlargement, and shifts from a lateral to a terminal position on either side of the primary telsonic fork, where its members constitute a secondary, and more conspicuous, fork, corresponding to the definitive caudal styles of Branchiopoda in general.

In this connexion the telson of *Apus* and of young *Lepidurus* (before the outgrowth of the dorsal plate) is of some importance, for, on the dorsal side, in addition to a pair of postero-medial lobes, each usually bearing a single strong tooth, like the primary fork of *Lepidocaris* [31, Pl. 35, and 4, Fig. 30], there is a peculiar

pair of small round plates sunk within a circlet of spines, half-way between the last abdominal ring and the base of the cercopods, one on each side [*Apus*, 16, Fig. 2; *Lepidurus* 23, and 16, Pl. 8]. Each of these plates bears a single long sensory seta, best seen in the larva. In the light of *Lepidocaris* the suggestion may well be hazarded that these sensory plates, though dorsal, may be the stunted remnants of an anterior pair of cercopods, in which case the telson of Notostraca retains to-day the precise constitution of the Devonian fossil. Homologues of the two setae are conspicuous in Conchostraca and Cladocera as the so-called 'caudal setae' [5, Figs. 17, 18].

It is interesting to recall that Bernard gave an accurate account of the anterior or dorsal 'cercopods' of *Apus*, and claimed them, with the posterior cercopods, as homologues of the four anal cirri of certain Polychaetes [1, pp. 20, 85].

In most Anostraca the telson is short and has every appearance of simplicity, but in *Branchipodopsis* a pair of dorsal spines may be the last relic of the peculiar denticulate plates of *Apus* [10, Fig. 50], and Packard's figures of the caudal fin of *Thamnocephalus* [31, Fig. 23] are strongly suggestive of a complex telsonic structure, similar to the pygidial plate of *Paradoxides* [43, Fig. 1369]. The fin of *Thamnocephalus* is certainly not a mere supra-anal plate, as Calman has interpreted it [5, p. 35].

We have suggested that the Trilobites which gave rise to the Branchiopoda were the Mesonacidae of the Lower Cambrian [40]. In the vermiform character of their tail-ends they were as unique among Trilobites as are Branchiopods among Crustacea, and both display the same anomomeristic character in trunk and tail alike. But there is one remarkable difference. Although the range in number of the trunk somites (i.e. pregenital in Branchiopods, or with complete pleura in Mesonacids) was much the same in Mesonacids as it is to-day in Branchiopods (11–19), it was more continuous, since the modal numbers (14, 15) were normal for Mesonacids, but are missing among Branchiopods. Now this number of trunk somites—14 with a compound telson, or 15 with a simple one—must have been fixed in any possible ancestor of the nomomeristic Malacostraca, and if either of these groups, Mesonacids or Branchiopods, included the ancestor, this fixed number must have been combined with a complete obliteration of the vermiform tail

region. Among Branchiopods, apart from the paedomorphic Cladocera, there is no example of any such reduction. On the contrary, if we are right, in the absence both of pleurites and pro-epipodites, in taking the post-genital somites of *Apus* and the Conchostraca as corresponding to the 'tail' of *Lepidocaris*

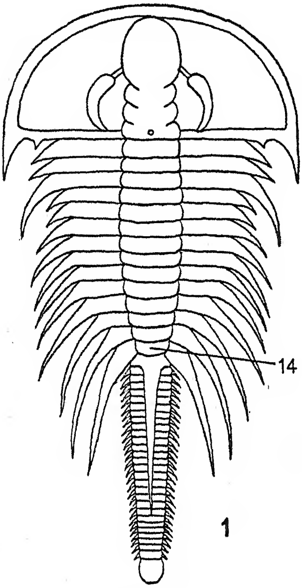

FIG. 1. *Paedumias robsoni*, a long-tailed Mesonacid.

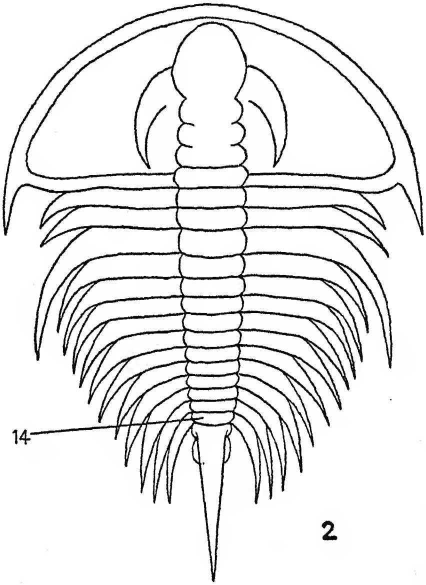

FIG. 2. *Olenellus* sp., a short-tailed Mesonacid.

and Anostraca, they display a marked tendency to retain this region as an integral part of their organization. Combined, as this feature is, with the absence of any example of a trunk of 14 or 15 segments, the possibility of any Branchiopod, even the most primitive, having given rise either to Leptostraca or Malacostraca is remote.

On the other hand Mesonacids with 14 trunk somites show the widest variation in the number of imperfect tail-somites, from about 30 in *Paedumias* [4] through 11 in *Mesonacis*, to a mere vestige of 2 or 3, possibly only one, in *Olenellus* [35, 40]. In their own ranks, therefore, while fully retaining their Trilobite characters, they have accomplished the essential part of

the change from irregular to fixed segmentation which lies at the base of Malacostracan organization.

In *Olenellus thompsoni*, according to Walcott, the caudal, or 15th somite carried a large terminal spine, the last relic of a dorsal segmental series in its immediate predecessors. This somite, with which the telson was presumably fused, bore no pleura, as already indicated, and was thus a remnant of the original Mesonacid 'tail'. Resser, however [35], now includes in the genus specimens with a few rudimentary somites between the spine and the telson. Owing to the stoutness of the spine and the slightness of the 'tail' it may be difficult to establish a case of complete obsolescence.

Now it cannot be without significance that both in *Nebalia* and *Mysis*, as Manton [28] has demonstrated, the abdomen includes a more or less rudimentary 7th somite which lacks appendages in both types, and in *Mysis* ultimately fuses with the 6th somite which bears the uropods. This abnormal somite corresponds to the 15th (spine-bearing) somite of *Olenellus*, and as Ceratiocarids with a caudal spine on the same somite, between a pair of furcal styles, were abundant in the Ordovician, a Phyllocarid line of descent from *Olenellus* to *Nebalia* is at once indicated. We suggest that *Nebalia* owes its limbless somite to its Ceratiocarid ancestors, but has discarded the dorsal spine to which the somite owes its original preservation. There are grounds for the belief that Copepods and Cirripedes may be offshoots of this series.

What then of the true Malacostraca, which bear such close relationship to *Nebalia*, and yet apparently cannot be linked to the Phyllocarid line either as offspring or as progenitors? They seem to have arisen suddenly, armed with their 'caridoid facies' and tail-fan, like Athena from the brow of Zeus—an example of that 'explosive Entwicklung' which Beurlen has theoretically illumined, and which one of us has already exemplified in this and other groups [11–14].

Summing up, we conclude that Crustacea were not derived directly from Annelids, or along with Trilobites from a common Annelid ancestor, but from Trilobites themselves as two distinct strains (diphyletic). Branchiopoda arose from typical anomomeristic Mesonacida of the Lower Cambrian, and Phyllocarida almost certainly from the later Olenelline branch,

in which the body had already acquired the fixed number of 14 trunk somites, together with an incomplete 15th somite, devoid of pleura, but carrying a terminal dorsal spine. The origin of typical Malacostraca cannot be far removed from that of Phyllocarida, but needs an ampler consideration of the whole life-history than we can enter upon within the limits of this essay.

Significance of Descent from Trilobites

Hitherto the study of Crustacean phylogeny has been largely influenced by the assumption of an immediate Annelid ancestry, and authors have appealed to the Annelid parapodium as determining the 'primitive' features of this or that type of Crustacean appendage, needless to say with very inconsistent results. The odds have been heavily weighted in favour of the 'phyllopodium' by the fact that Branchiopods retain the Annelid features of a multiplicity of somites and a general uniformity of their appendages. This question is now settled by the fact that Trilobites combine segmental indeterminism and appendicular uniformity with a biramous foot which is as far from foliaceous as it could be.

Another element has been the long-lingering faith in the recapitulatory nature of development, so that to some authors the seemingly equiramous swimming feet of nauplii and zoeas have suggested pelagic ancestors with actively rowing habits. This view also must now be abandoned, for the Trilobite foot was not a two-bladed oar or 'copepodium' but a 'mixopodium', one half ambulatory, the other vibratile, which means that the appendages of Crustacean larvae have deviated from the original type by undergoing secondary larval modifications (see below).

'Every theory of evolution', says Professor Goodrich, 'must be tested by the results of palaeontology; no conclusions can be accepted which are inconsistent with them' [15, p. 153]. We must be satisfied, however, that the 'results of palaeontology' are not transitory misinterpretations. One such is exemplified in current accounts of the Trilobite leg. Why is the so-called 'coxopodite' accepted as such? Simply on the analogy of the gnathobase of *Apus*, which was formerly regarded as coxal. And why are the remaining segments labelled basis, ischium,

&c.? Merely to conform to the legs of the lobster. Granted the coxa, the rest inevitably followed in 1893–5. Since then, however, Coutière and Hansen have shown that primitive Malacostraca (*Nebalia*, *Anaspides*, &c.) have an extra segment in their endopodites (pre-ischium), making 6 segments instead of 5, i.e. 7 segments with the distal segment (basis) of the protopodite. That is precisely the number invariably shown by the legs of Trilobites—an endopod of 6 simple and identical segments, together with a basal segment to the distal end of which both endopod and exopod are articulated. *This segment is therefore the basipodite, not the coxopodite.* A strong gnathic process of the basipodite is of course an essential feature of the maxillule throughout Malacostraca. It is also a distinct, but weaker, element in every maxilla, and is usually recognizable in the first maxillipede, in which appendage it may even assume renewed importance.

Moreover, Hansen's figures [22, Pls. III, IV] strongly suggest that in the highly modified but ancient group Ostracoda three stages are still preserved in the gradual replacement of a primitive basipodial by a later precoxal jaw. In the mandibles of Myodocopa the basipodial element still predominates in *Conchoecia*, though reduced in *Cypridina* and *Polycope*, while in Podocopa (*Macrocypris*) it has vanished completely, and the precoxal *corpus mandibuli* has attained its typical form.

The articulation of the limb with the body is still obscure, though we agree with Walcott [42] that Raymond's 'appendifer' theory, and his reversal of the gnathobase to suit it, have no foundation. What is certain is that there was no substantial coxal segment, merely a short articulating membrane between basipodite and body wall. The long protopodite of Branchiopods and the hard angular coxal joints of Malacostraca have arisen since Crustacea broke away from their pleuron-bearing ancestors, and used their legs more freely. We have called the Trilobite's endopod 'ambulatory', but it is not implied that its ambulation was of the same nature as that of a prawn or a crab. From its straight, transverse articulations its motions must have been mainly to and fro, small in extent and weak in power.

Early Trilobites, with which alone we are concerned, were clearly not pelagic but benthic, probably swimming on their backs near the bottom [37], and turning over from time to time

to skim the fine Cambrian mud with their protopodial endites, much as existing Branchiopods do [26]. This mode of swimming has persisted, not only in the Branchiopods, but also in many larval Decapods.

The Nauplius a specialized Protaspis

The Entomostraca and certain Malacostraca pass through a free Nauplius stage. Other Malacostraca exhibit a more advanced type of free larva, the Nauplius stages being passed in the egg; but even these often begin their free life by moulting the old Nauplius skin [19]. In extreme cases the whole development may take place in the egg, and be seemingly direct, but pauses in the development mark the passage of old larval stages, sometimes accompanied by the moulting of old larval skins, of which the Nauplius is the most constant. It is therefore universally agreed that a Nauplius was the larval stage of all the earliest types of Crustacea.

'Similarly', says Swinnerton, 'the egg of the Trilobite evidently hatched out at an early stage in the development, for the youngest-known larvae differ greatly from the adult' [39, p. 248]. 'These', says Raymond, 'are little discoid or ovate bodies not more than 1 mm. in length. This first larval form has been named the *protaspis*, and has been found to be the larval form characteristic of all Trilobites' [43, p. 703]. Korschelt and Heider cite evidence from Barrande which renders it probable that some of the less primitive Trilobites, like the higher Crustacea, may suppress the earlier larval stages.

There is thus a close parallel between Trilobite and Crustacean ontogenies, and our next task is obviously to see whether the Nauplius is more or less primitive than the Protaspis, and derivable or not from it.

Again we quote from Professor Goodrich:

'A fish, a reptile, a mammal, each develops from an egg composed of a special specific substance, each is fish, reptile, and mammal respectively from the beginning; hence no stage in the ontogeny of one is really the same as any stage in the ontogeny of the others, nor can it recapitulate the adult stage of an ancestor. . . . Owing to divergencies in adaptation the ontogeny may deviate from that of the ancestor at any stage, and often to a remarkable extent' [15, p. 147].

We begin with the Protaspis, and for illustrations and additional detail refer to Korschelt and Heider [24], Raymond [34], and to Swinnerton's brief but lucid sketch [39]. In addition to these authoritative summaries we have also made use of the data in a group of recent papers by Raw [32], who deals with a series of early Trilobites of special interest to us, and carefully figures successive stages of the Mesonacid *Olenellus* (Lower Camb.) which we have mentioned earlier, two species of *Paradoxides* (Middle Camb.), and an Olenid, *Leptoplastus* (Upper Camb.), related to Barrande's *Sao*, the ontogeny of which is figured in every text-book.

From all these sources it is abundantly clear that the development of Cambrian and most later Trilobites was essentially direct or determinate, with only the slightest of transitory deviations subservient to larval ends. In some post-Cambrian forms additional modifications arose which complicated their development, e.g. precocious development of the eyes in front (*Proetus*, *Dalmanitina*, &c.), but in the earlier Cambrian forms, from which alone the Crustacea can have arisen, the only established deviations are in the temporary elongation of particular cranidial and pleural spines in the intermediate larval stages. These are, in Mesonacids, the metacranidial and 3rd pleurals [cf. 24, Fig. 328; 32, Figs. 23–5]; in Paradoxids the 1st and 2nd pleurals successively, together with the metacranidials [32, Figs. 13, 14, 16–20]. These very transitory modifications are readily interpreted as larval adaptations for flotational (anti-gravitational) purposes, and disappear completely in later stages, like the spines and thorns of many Crustacean larvae. They afford reliable evidence of a temporary pelagic phase in the forms which display them.

It is quite in keeping with this phenomenon that the nepionic stages of the Olenid *Leptoplastus*, as described by Raw ([33] Figs. 6, 7), should exhibit relatively longer spines than the adult. On the other hand, we find nothing in the development of *Olenellus* to support Raw's theory that the genal spines of this Mesonacid are procranidials which have rotated phylogenetically or ontogenetically from the front to the back of the head. No reasons are given to show that the so-called 'parial' spines of the second stage (Fig. 23) are not simply the metacranidials of the first stage (Fig. 22) carried outwards by a

marked extension of the base of the cranidium, and temporarily elongated like those of *Paradoxides*. If this be so, Raw's fancied 'procranidials' are in fact the true parials, growing from the usual place at the usual time, and lacking only a facial suture to enclose them, the absence of which is a primitive character of all Mesonacids. This case, accordingly, cannot be cited as an exception to the rule of direct development in early Trilobites.[1]

We are thus justified in equipping the Mesonacid Protaspis with precursors of the normal 5 pairs of head appendages of the adult, and these must have been distributed evenly along its length, diminishing slightly in size from before backwards, in accordance with the evident segmentation of the head [24, Fig. 328; 25, Fig. 8]. Then the tail-piece developed a series of rudimentary somites, and complete 'pleural' somites were added one at a time afterwards. Raw states that the full 'number of thoracic (i.e. free) somites is in all normal Trilobites relatively early acquired, when as yet the length is only a fraction of that to which it can grow'.

Now the Nauplius, while closely similar in shape and size, and initiating a closely similar ontogeny, differs from the Protaspis in two obvious features. It does not show the quinquepartite segmentation, and bears only three pairs of appendages. It is therefore usually regarded as something lower and more primitive than the Protaspis. We dissent from this view for several reasons: Firstly, it cannot be urged that absence of segmentation in an Arthropod with three pairs of appendages is primitive. Secondly, the distribution of the three pairs of appendages in the Nauplius indicates that its body includes a large posterior region additional to that which corresponds to the three segmental appendages present. For evidence we refer to almost any reliable picture of a first-stage Nauplius, but in particular to A. G. Nicholls's recent account of the Copepod *Euchaeta norvegica* [29, Fig. 2], Lebour's account of the Euphausids of Plymouth, especially *Meganyctiphanes* [25, Pl. 4], and Macdonald's of *Thysanoessa* [27, Pl. 1]. The three pairs of appendages radiate from the mouth in the anterior half of the body, leaving the posterior half quite bare. Compare these pictures with Korschelt and Heider's of the Protaspis of

[1] For a fuller criticism of Raw's theory see Stubblefield [38].

Elliptocephala (*'Olenellus'*), and the significance of the difference is apparent. Thirdly, in *Longipedia*, possibly one of the most primitive of all Copepoda, the first Nauplius possesses two long feathered setae in front of the tail-piece, which have been shown to be the rudiments of the maxillules [Gurney, 20, Fig. 1; Nicholls, 30, Fig. 2]. It is possible that the minute hairs sometimes present in the same position in some first-stage Cyclopid Nauplii may also represent the incipient maxillules [21, Figs. 1245, 1331]. These appendages make their first obvious appearance in stage II of Cyclopids and Harpacticids, and in stage III of Calanids. In no case, however, are they fully formed and functional before the last of the 5 or 6 Nauplius stages which occur, for their endites are lacking until the Copepodid stage. These variations in the time of appearance of the maxillules strongly suggest a progressive retardation from a primitive condition when they were always present in the first Nauplius. In any case the presence of rudimentary maxillules in the first Nauplius of even a single genus of Copepods disproves the assumption that only three somites are represented in it. The 'head capsule'—to borrow an entomological term—is complete, but mesodermal activity in its maxillary region is temporarily suspended [good evidence of this is to be found in Cannon, 7].

The fact is that in the Nauplius stage, while the antennae are still adoral in position and armed with basal gnathites, the three pairs of appendages form a closed system, sufficient in itself both for locomotion and feeding, while the maxillules and maxillae demonstrably undergo a different specialization of form and function useful only in the later stages of development. A division of labour between the five pairs of head appendages, so that the first three serve the larva and the last two are retarded to serve the adult would have many analogies, e.g. mandibles serving the caterpillar and maxillae reserved for the butterfly.

With these considerations in mind we suggest that the differences between a Nauplius and a Protaspis are due to a progressive retardation of the post-mandibular appendages in the former, and not to any initial difference in constitution. In the presence of vestigial maxillules in the first Nauplius of *Longipedia* we have a last relic of an original Protaspis condition,

in which a pair of antennules and four pairs of uniform biramous appendages were present. In the later Nauplius stages of *Longipedia* the uniformity of the biramous maxillules with the antennae and mandibles is admirably displayed in Nichols's sketches [30, Fig. 2]. It is also manifest from his drawings that all three appendages in the Nauplius stages are constructed on the lines of a Trilobite's appendages, viz. an endopod of broad joints tufted with setae on their internal edges, and a flagelliform exopod of more numerous short segments, each with a single long seta internally. The endopods are not miniatures of the adult structures, but rudimentary, as they doubtless were in the Protaspid larva, and the amount of segmentation which they exhibit diminishes regularly from front to back—three imperfect segments in the antennae, two definite segments in the mandibles, and one only in the maxillules, and that not separated from the basis.

This inequiramous type of appendage is also characteristic of the Nauplii of Cirripedes and Penaeids, and persists throughout the Protozoea stages both of Penaeids and Caridea, though with a progressive reduction of the original segmentation, both of endopod and exopod [19]. It is recognizable also in the larvae of most Branchiopods, and is especially clear in the Protaspis-like Nauplius of *Limnetis* [Gurney, 18], but is disguised in most Branchiopods by the lack of segmentation and the extreme elongation of the protopodite as an 'outrigger'. In Euphausids, which use the antennae for rowing almost to the adult phase, a seemingly equiramous and simple condition is assumed from the start, each branch beset with a terminal tuft of bristles, and this condition is retained until the last Furcilia stage. The exopod, however, betrays the inequiramous constitution by showing a minutely segmented tip [25]. Only in Conchostraca and Cladocera, which retain locomotive antennae throughout life, are the antennae fully transformed into equiramous appendages. Even *Lepidocaris*, which used its antennae in the same way, retained a clear differentiation between the two rami, although the process of assimilation had obviously begun.

All these facts, so unintelligible if the original limbs are assumed to have been equiramous or foliaceous, fall into line at once when it is recognized that Crustacea originated from

Trilobites, and that the Nauplius larva is a modified Protaspis, secondarily reduced and more highly specialized for a planktonic career.

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SOME ASPECTS OF EVOLUTION IN ECHINODERMATA

By W. K. Spencer

Material

FOSSIL Echinodermata, because of the characteristics of their skeleton, offer very good material for study. The skeleton is an endoskeleton which carries on the outside of its plates depressions and protuberances which allow the study of the insertion of the muscles, the course of nerve strands and of the vascular system. At the same time, since the skeleton conforms in general to the body outline it is possible to reconstruct the entire original outlines of the animal and speculate upon the relationship of form to habit. A further valuable character is that the mineral content of the plates is almost entirely calcium carbonate, which upon solution by underground waters leaves moulds showing in faithful reproduction all the minute structure carried on the surface of the original plate. Guttapercha casts of these moulds are far easier to study than are undissolved specimens, for in these post-mortem mineralization hides much detail.

Much of the Palaeozoic material is found in thin beds which are isolated in great vertical masses of barren rock. These beds show all the characters of an old sea-bed which has been overwhelmed by sudden catastrophy under conditions which have preserved the animal inhabitants very perfectly. Often the animal seems to have been killed whilst in a posture showing strong resemblances to those seen in kindred forms of the present day. These 'fossil postures' are a great help in the interpretation of the fossil plates in relation to the original soft parts.

Linkage with knowledge of recent forms

There is an increasing body of knowledge of method of feeding and of habit in relation to environment which is of great assistance to the palaeontologist.

Sources of food. The great majority of the Echinoderm groups feed on small food particles. Two important sources are:

(*a*) the rain of plant debris which is constantly sinking

through the water. There is now and always must have been a large quantity of food available in this food shower. Petersen [11] has shown that at the present time the quantity of plant food available from the decay of the sea-grass Zostera growing in the Skaw is equal to three times the amount of meadow hay in Denmark.

(*b*) bottom-living diatoms. These are particularly abundant amongst sand. Remane [12] lays particular emphasis upon the diatoms as a food-supply, pointing out that even in the region of coarse sand practically every sand grain of the surface layer is adorned with several diatoms, and in the regions of fine sands in smooth water, diatoms, together with peridinians, form a brown layer that has introduced the term 'diatom sand' for these regions.

Methods of feeding. Remane suggests the following grouping for animals which depend upon the collection of fine particles:

1. *Whirlers.* Cilia produce an eddy in the surrounding water, in which particles are eventually caught by other cilia, and, helped by a secretion of mucus, conducted into the place of digestion.
2. *Filterers.* A stream of water is produced and passed through a hair sieve or rigid network. Cilia are used neither as producers of the water stream nor as collectors of particles.
3. *Feelers.* Animals that search the surface of their surroundings with long tentacles, which they also use to carry food particles to the body.
4. *Sedimenters.* Food material, deposited on outstretched tentacles (or long hairs) is helped into the mouth mostly by licking. Assistance of particles by production of a stream of water never occurs, only particles deposited accidentally on outstretched processes are taken in.

The Echinodermata are never filterers but may belong to any of the three other groups. 'Whirling', as will be shown later, appears to have been the method of feeding of the extinct Palaeozoic groups—the Cystoidea, Blastoidea, and Edrioasteroidea. Starfish are 'feelers', Holothurians are 'sedimenters', as probably were also the extinct group the Carpoidea (see p. 296)

Mode of life. The current subdivision of the Echinodermata is based upon the mode of life. It is as follows:

Pelmatozoa (sessile forms)	*Eleutherozoa* (freely moving forms)
Cystoidea, including Blastoidea (fossil only).	Asterozoa (fossil and recent).
Thecoidea, Jaekel = Edrioasteroidea, Bather (fossil only).	Echinoidea (fossil and recent).
Carpoidea. Jaekel (fossil only).	Holothurioidea (fossil and recent).
Crinoidea (fossil and recent).	

All the extinct groups of Echinodermata were sessile or semi-sessile, and amongst the Eleutherozoa the Asteroid, during its development, may also pass through a sessile stage. There is every probability that the original Echinoderm was sessile.

Ontogeny teaches us that the attaching organ was developed from the pre-oral lobe; its degree of development varies very greatly: 1. In the Eleutherozoa it is only present in Asteroidea and then only in the early stages before metamorphosis. 2. In the Crinoidea it becomes a well-calcified stem which holds the animal upright. A basal attaching organ roots it to the sea-floor. An important nerve system is also carried by the stem. 3. Many Cystoidea and Blastoidea also develop a well-calcified stem with a basal attaching organ. In some Cystids the stem is short and shows itself to be merely a prolongation of the theca. The stem is still more reduced in the Edrioasteroidea, where there is usually only an attaching organ and only very exceptionally a prolongation of the theca. The earliest Edrioasteroidea seem to have been able to fix themselves to a sandy bottom; later the forms are found almost exclusively on shells. Many acquire a habit of confining themselves to shells of one species which definitely classifies them as epizoa. 4. The extinct Carpoidea have no organ of attachment at the end of their well-developed stem. These forms were not erect but lay on their sides at the bottom, and the stem was used as an anchor (see p. 294).

Remane [12] points out that sessile animals are almost entirely restricted to the phytal zone, a fact that no theory on the origin of the sessile mode of life should ignore. It may be that the history of the Echinodermata is a history of migration

from the phytal to other zones. Nowadays the common starfish *Asterias* passes the stalked stage of its development in the phytal zone.

Respiration. Very few vessels which are at all comparable to arteries, veins, or capillaries are present in the recent Echinodermata, and there are no respiratory pigments. Apparently oxygen is conveyed to the tissues by the general fluid of the coelom, which is kept in slow motion largely by ciliary action. In the young stages a pulsating vesicle—the so-called Echinoderm heart—aids this motion.

Some of the extinct forms had their own method of conveying oxygen from the exterior to the coelomic fluid. Thin-walled pouches were driven through the thecal wall, and projected well into the interior. A constant stream of sea-water was driven through the pouches. Billings called these pouches 'hydrospires'. Very often they are arranged in parallel with a general disposition well described by their name 'pectinirhombs'.

Generally (except for the Ophiuroidea) the Echinodermata are slow-moving animals, and this method of respiration suffices. A suggestion is made later (p. 293), however, that the ancestral Echinodermata may have had a much more extensive 'vessel' circulation.

Asymmetric growth

There is a tendency, especially noticeable in the tentacle-bearing Echinodermata, to develop asymmetries. Thus in all recent forms it is only the left hydrocoel which gives rise to the tentacles, the right hydrocoel never taking on this function. The Carpoidea develop similar asymmetries in relation to the respiratory organs and the place of origin of the stem.

Podaxonid growth

The alimentary canal, even at its beginning, has a strong curvature; the animal is 'hump backed' (Gislén [6], p. 213). This curvature is increased in many forms by the main rate of growth being in a direction almost at right angles to the line joining mouth and anus. In consequence the mouth and anus remain closely approximated whilst the form becomes at the same time very steep sided. This 'podaxonid' type of growth is similar to that in the Phoronids and the Polyzoa, which also are sessile.

The fossil forms chosen for description suggest

(1) that at one time Echinodermata existed which had no tube-feet. These were 'whirlers', extracting their food from the sea-water by ciliary methods very similar to those shown at the present day by very various groups, the Polyzoa, Brachiopods, Lamellibranchs, Sabellid worms, &c.

(2) that the Echinodermata which possessed tube-feet probably arose as 'sedimenters' from forms similar to the Carpoidea. A new interpretation of the structure of a Carpoid is given.

The Sessile Echinodermata and their mode of feeding (Plate 2).

Sessile Echinodermata now are a comparatively insignificant group, but they were very abundant in the older Palaeozoic seas. The Trenton rocks of Ottawa, e.g., contain beds of from six inches to three feet composed almost entirely of separate ossicles of species of *Steganoblastus*, and the Crinoidal beds in Palaeozoic limestone are a well-known feature.

Food capture in the sessile Echinodermata is nearly always effected by means of a wide funnel which faces the food shower descending through the sea.

In the recent sessile Echinodermata this funnel is composed of arms which take origin at the top of the calyx and carry on them very numerous tentacles which capture suitable food particles and hand them into ciliated grooves (ambulacral grooves) occupying the middle of the arms and their side branches (the pinnules). This groove carries cover-plates.

The funnel of the Cystoidea, Blastoidea, and Edrioasteroidea has at first sight many resemblances to that of the Crinoidea, but really is composed of parts differing anatomically in origin.

The arms (brachioles) which make up the funnel in the majority of the specimens seem to have ambulacral grooves and cover-plates. Well-preserved specimens show, however, that this groove was closed completely. The covering of irregular small plates is quite dissimilar to the cover-plates of the Crinoidea, and it would have been quite impossible for any tube-feet, if they had been present, to emerge from the groove. The mouth is also roofed over. The whole therefore of the 'so-called groove system' consists of covered channels, and a study of the

minute structure of specially well-preserved specimens shows that the entrances to the main channels were by minute side-channels which in their turn led to the base of the brachioles. The interpretation I am giving is that the brachioles were covered with cilia which, like the cilia on the lophophoral tentacles of the Polyzoa, created food currents which were filtered by minute holes at the base of the brachioles before entrance to the main food stream. The filtered food stream is dragged through the holes by cilia within the covered channels. This method of filtering is very similar to that found in sponges. The complete roofing of the mouth is a further device to exclude the coarse particles. Studies on ciliary feeding of recent forms show that precautions are always taken to exclude coarse particles. Further evidence that this interpretation is correct is given by the presence of lateral grooves between the brachioles which clearly make a path of exit for the rejected coarse particles.

The food-collecting apparatus of the Cystoidea which concentrate their brachioles around the mouth have superficial resemblances to that of the Sabellid worms. In these the gill filaments form a projecting funnel just as do the brachioles of the Cystids. The separation of the coarse from the fine particles is carried out in narrow grooves at the base of the gill filaments before the food stream can reach the mouth. The so-called hydrophores palmées of Barrande are narrow grooves placed between the base of the brachioles and the mouth which could have served the same purpose.

The Cystoidea must have fed from the food shower descending through the water, and the large surfaces of their brachioles enabled them to extract this finely divided food from the sea-water. Like all ciliary feeders they were able to deal with large masses of sea-water. Bidder ([4], p. 129) has pointed out that amongst recent forms the sponge *Leuconia*, an animal half as large again as a finger, moves a ton of water every eight days. This method of feeding is in strong contrast to that suggested below for the Carpoidea.

The vascular system of some primitive Cystids

Some Cystids show a system of tubes passing through their skeleton which seem to have had the function of bringing body fluids into contact with an outer 'epidermis', which also is peculiar

to these forms. These Cystids have no hydrospires, and it may well be that this tube system and the well-developed 'epidermis' were concerned with respiration.

We owe almost all we know about these tubes to Barrande [2], for later authors have tended to refuse to give serious attention to his descriptions. A few Bohemian specimens have passed through my hands, and I am able to add to the account given by Barrande. Very fortunately the post-mortem changes which these Cystids have undergone facilitates the study of the tubes. The first stage after the animal died was the decay of the soft tissues within the skeleton and the filling in of the consequent cavities by fine sediment. By this means the tube system became preserved as mud casts running through the skeleton. The second stage was the solution by underground water of the calcite of the main mass of the skeleton. The casts now remained as hard mud strands in cavities at one time occupied by skeletal plates. They are seen very clearly whenever the cavities are exposed.

My colleague Mr. Heasman has pointed out to me that both the build of the skeleton and this tube system have a strong resemblance to that of the exo-skeleton and so-called exo-skeletal vascular system of the Cephalaspids. In both cases

(*a*) there is a thin outer layer exterior to the 'bone'. Stensiö states that in the Cephalaspid fish this is dentine which near the surface approaches enamel in character. In the Cystids Barrande called it 'epidermis'. It is not dissolved away by underground water as the calcium carbonate of the 'bone' is, but remains as an outer capping to the empty moulds which represent all that is left of the original 'bones'. The layer is very readily recognizable in *Aristocystis*.

(*b*) the arrangement of the tubes follows the 'area distribution' of the 'bones' of the skeleton. In *Cephalaspis* the areas are so called polygonal areas—the corresponding areas in Cystids are those of the separate ossicles. A circular sinus surrounds each polygonal area in *Cephalaspis*, and I think that I can recognize this same sinus in *Arachnocystis*.

(*c*) The tubes are of two types, vertical (centripetal) and horizontal. The vertical tubes in Cystids issued from the

cavity, representing the original body organs; in Cephalaspids they also arise from underneath the skeleton, from the aponeurotic venous system of Stensiö. The horizontal tubes lie immediately under the outer layer in both Cystids and in Cephalaspids. Clearly this part of the system is that most intimately concerned with the collection of oxygen from the exterior. In *Arachnocystis* these horizontal tubes stretch from the plate boundaries well towards the middle of each plate. There is here an especially marked resemblance to the radiating canals of Stensiö.[1]

Semi-sessile Echinodermata and their mode of feeding

Remane [12] defines semi-sessile animals as animals which remain fixed for a long time in one place from which they do not wander in search of food. They can, however, leave this place either if their environment is unfavourable or, for purposes of reproduction.

Jaekel ([7] and [8]) separated from the Pelmatozoa a new Class, the Carpoidea of which three Orders, the Cincta (*Trochocystis* and its allies), the Mitrata (*Mitrocystis* and its allies), and the Cornuta (*Cothurnocystis* and its allies) fall into this category. The fourth Order, the Soluta (*Dendrocystis* and its allies), appear to me not to belong here.

The characters of the three Orders as given by Jaekel can be summarized as follows:

1. The stalk is not composed as in sessile Echinodermata of a row of rounded stout columnals which hold the animal firmly upright in the water. Instead it is flattened and tapering, often with a proximal hollow which at one time contained a muscle.
2. The theca is conspicuously flattened and lay parallel to the bottom, with the stalk projecting as an anchor. The muscle inside the stalk allowed rotatory movements of the theca, the anchor serving as a fulcrum.
3. There are no signs of the former presence of brachioles; that is the animal could not filter large volumes of water. Often there is only one opening concerned with nutrition.

[1] Material for the further study of this system can best be seen at Prague and at Rennes, and I am hoping later to make a more detailed investigation.

Jaekel interpreted this as an anus, suggesting that anal feeding became possible because the animals like the recent Holothurians took in water through the cloaca for respiratory purposes. Since this water contained food particles there arose a more efficient process of food intake than by ciliated grooves.

Gislén [6] more recently has accepted Jaekel's separation and also the suggested method of feeding. He would allow certain of the forms the power to take up their anchors and swim.

The two groups of Carpoidea described here are the Trochocystids and the Cothurnocystids.

Trochocystis and its allies (Plate 1).

Trochocystis Barrande, and its allies *Gyrocystis* Jaekel and *Decacystis* Gislén, are the oldest-known Carpoidea. They occur exclusively in the Middle Cambrian. *Trochocystis* is from Bohemia, *Gyrocystis* from the south of France, *Decacystis* from Spain. The account given below is based upon numerous specimens of *Gyrocystis* preserved in the Museum of the University of Montpellier and in the British Museum of Natural History. Most of the specimens have been listed as *Trochocystis barrandei* Munier—Chalmas and Bergeron. The type of this species, however, is merely *Gyrocystis* in an imperfect state of preservation.

The theca of all three genera is flattened and the edge is strengthened by a framework of twelve thick marginalia, six on each side. In cross-section each marginal is shaped like a runner of a sleigh, the under broad surface no doubt preventing the animal from sinking in the mud. This marginal frame supports two integuments. The integument which lay against the sea-bottom was occupied by stout closely-fitting plates. The integument away from the sea-bottom had the majority of its calcifications small and loosely joined, these are rarely preserved. A portion of the integument near the oro-anal pole was, however, stoutly calcified. The character and disposition of these ossicles, as will be shown, is of great importance.

The oro-anal pole has two openings which pierce the marginalia on the thecal edge. One opening is large and bounded by marginalia 5_1, 6_1, and 6, the other is smaller and bounded by 5 and 6. The stoutly calcified ossicles have a definite relationship to these openings. The large opening is covered on its upper

face by an oval, swollen, pitted plate. Looked at from the front this plate is concavo-convex and shows a lower opening shaped very much like the almost shut operculum of a Polyzoan. At the distal edge of this large plate is a row of smaller plates. A small plate is placed above the smaller opening.

Jaekel, Bather, and Gislén have all called the large opening the anus and the smaller opening the mouth. The reason for this identification has been that in the Bohemian form, grooves could be recognized on the marginalia which led to the small opening. It was supposed that these grooves were similar to those ciliated grooves in Cystids which undoubtedly lead to the mouth. The grooves are much less pronounced in *Gyrocystis* and entirely absent in *Decacystis*. This loss of the grooves and of a ciliary feeding mechanism was co-ordinated with the transference of the food intake from the 'mouth' to the 'anus'. *Trochocystis* was in transition between ciliary and anal feeding.

Jaekel who discovered the oro-anal plates called the large operculum-like plate—the anal valve. He recognized, however, that this so-called anal valve was quite different to any known anal valve and therefore gave it a peculiar function, namely, to support a fringed soft skin which helped to collect food. Whilst serving this function the valve was swung outwards over the edge of the marginals ([8], Fig. 105 c, p. 114).

This manner of feeding is entirely different from any which can be observed in living forms. The following interpretation of the structure, on the contrary, can be matched in several groups.

The animal lived by 'tentacle feeding', the tentacles being placed in a stomodaeal pouch underneath the operculum (Jaekel's anal valve). The remainder of the oro-anal plates define the limits of the pouch, and some of them served as a hinge to the operculum. Several of the specimens show the way this stomodaeal pouch could have opened in order to allow the tentacles to emerge. Not only the operculum but also some of the marginalia took part in this movement.

A reconstruction of *Gyrocystis* would resemble in many respects a developing *Antedon* at the stage at which it still lies with its stalk parallel to the sea-bottom. The stomodaeal pouch of *Antedon* also has valve-like calcifications in its walls. Similar valves occur in the larval Holothurian (see p. 301).

The abundant material of *Gyrocystis* is very varied in outline. These various outlines suggest the way in which the animal could search the sea-bottom whilst still remaining semi-sessile. The form seems to have been able to change its shape very considerably. The condition varies from an extreme in one direction, an elongation along the axis at right angles to the stalk resulting in a kidney-like appearance, to a pronounced elongation along an axis in a direct line with the stalk, which makes the form look like a short worm. One is irresistibly reminded of the changes of shape of a Holothurian when it shortens its body by a shortening of its longitudinal movements and lengthens it by the squeezing action of its circular muscles. The shape changes suggest a possibility of exploration of the sea-bottom from a fixed point afforded by the stem anchorage. Thoral ([13], p. 33) points out that the stem usually is pushed into the sub-stratum almost at right angles to the body plane. The animal can thus be pictured as pushing its mouth forward now in this direction and now in that in search for food.

We can interpret the stem as a prolongation of the theca and its ossicles as being merely a continuation of the general skeleton. It is made up of a number of stout ossicles which are scarcely distinguishable from marginalia. These ossicles gradually diminish in width, the stem tapering gradually off to a blunt peg.

There is no evidence either of the differentiation of stem ossicles such as is found in the majority of the Carpoidea, or of any pronounced hollow occupied by well-developed musculature.

The smaller opening is the true anus. The figures show that a narrow tube must have enclosed the hinder end of the gut and given a jet-like character to the anal opening. The importance of a jet in the ejection of faeces has been well shown by Bidder [4].

The Trochocystids and the larvae of recent Echinodermata

It is possible to make comparisons between the larva of recent Echinodermata, e.g. that of a starfish, and of the Trochocystids as interpreted here without necessarily assuming that either give an exact picture of an ancestral Echinoderm. In the larva the mouth and anus are closely approximated and the intestine is

strongly curved. In the Trochocystids the mouth and anus are very near indeed to one another and the body-shape suggests a strongly curved intestine with podaxonid growth.

This comparison necessitates the view that the Trochocystids lay on their side with their true ventral surface on end. If we suppose that the form is in transition from feeding from the food shower to feeding from the bottom we obtain an explanation for the disposition of the mouth. It is exactly the same change as occurs in recent flat-fish. There is, however, this difference; a flat-fish is a pelagic form which has become a bottom feeder. The Trochocystids were probably sessile forms before they took to bottom feeding. It would be extremely difficult otherwise to account for the pronounced development of the stem if the immediate ancestor were pelagic, but it is easy if this ancestor had a previous sessile habit.

Concerning the origin of tentacle-feeding, the following suggestion can be made. Tentacles are analogous organs to brachioles, that is, they originally formed a feeding funnel comparable to the tentacles of the Polyzoa, which have been shown by Atkins [1] to be clothed with differentiated cilia creating a feeding current and at the same time collecting food from it. Since ciliary feeding is accompanied by the secretion of mucus the tentacles would become sticky and form admirable traps for food particles. The animals would thus become 'sedimenters' (see above, p. 288), that is, forms in which the food is deposited in outstretched tentacles and is helped into the mouth by licking. The tentacles can either project freely into the water or be smeared along the bottom. This is the manner in which Holothurians feed at the present day.

Cothurnocystis

Cothurnocystis was first described by Bather from the Starfish bed of the Upper Ordovician of Girvan. There it occurs in considerable numbers. More recently Thoral has found the genus in the Upper Cambrian of Hérault.

Cothurnocystis resembles *Trochocystis* in that it possesses the same bar-like marginalia. The frame, however, is boot-shaped, and is reinforced by a strut which stretches across the middle of the animal. Projections like the legs of a stool, placed on the marginalia, lifted the form from the sea-bottom. The upper

surface of the theca is perforated in two distinct regions: at the toe of the boot, and at the top of the boot leg.

The openings at the toe of the boot are narrow and slit-like. In one species, *Coth. elizae*, the slits are single, each being separated from its neighbour by calcified integument; in the second species, *Coth. curvata*, they are collected into one mass which forms a sub-triangular compact 'plate'. Bather ([3], p. 410) noticed the resemblance between this plate and a pectinirhomb, but gave it as his view that in both species the slits were a series of little mouths which eventually led to a pharynx. Bather was undoubtedly influenced in his view by his inability to find any other opening which could be regarded as a mouth, and his strong objection to Jaekel's suggestion that the animals fed through the anus.

Jaekel's view that the Carpoidea fed through the anus was based on studies [7] which preceded Bather's description of *Cothurnocystis*. Later [8] he still stuck to his views on the method of feeding and suggested that Bather's slits were gonopores.

Gislén ([6], p. 221) in his interesting comparison with the primitive vertebrates, found resemblances between these slits and gill-slits although he gave a nutritional rather than a respiratory function to them. They were drainage organs for excess water taken in during anal feeding.

I propose in a later communication to show that these slits are respiratory pouches probably without any communication with the alimentary canal. I cannot therefore support Gislén.

The opening at the top of the boot leg was undoubtedly concerned with food intake and faeces disposal. Here the plates are all minute and arranged in radiating lines which converge to a point in the middle of the leg and more or less on a level with the top of the frame (Bather [3], p. 399). Bather, Gislén, and Jaekel have all interpreted the radiate wrinkling of the integument as indicating an opening with a sphincter muscle, and have made a further suggestion that such an opening must be an anal opening.

In my view this sphincter muscle is a muscle closing the mouth of a vestibule which held mouth and anus. The account given of the Trochocystids shows a podaxonid method of growth. A further extension of this mode of growth, just as seen in the Polyzoa and in the Phoronidea, would bring the mouth and

anus so near to one another that only one opening could be recognized. This, as in *Trochocystis*, is at the edge of the frame, and it would be easy for tentacles placed in such a vestibule to search the surrounding mud. Anchorage in *Cothurnocystis* is given by placing the distal extremity of the stem at an angle. That limited movement from this fixed point was allowed is shown by the structure of the proximal stem region which suggests the possession of a large muscle. The stem segments can be seen to be drawn together, concertina-like, in some specimens by such muscle action whilst remaining more open in other specimens when presumably the muscle had relaxed.

Cothurnocystis is undoubtedly a more highly specialized type than *Trochocystis*. It is accompanied in the Lower Ordovician by related genera which include *Placocystis* Thoral. These genera are later than *Trochocystis* and seem to have reached West Europe in the same inflow which brought the most primitive starfish.

The semi-sessile ancestors of the Eleutherozoa and of the Crinoidea

The Carpoidea (*sensu stricto*) have specializations which render it impossible that they were ancestral to either the Eleutherozoa or the Crinoidea.

The hypothetical ancestors of these must, however, have had many characters possessed by the Trochocystids. Their evolution may have been as follows:

1. The mouth and anus, which, in *Gyrocystis* were still in the larval position relative to the general body-surface, migrate to adapt themselves further to the new conditions. Their best positions clearly are those in which the mouth faces directly downwards towards the food-supply, and the anus is placed to direct the faeces away from this supply. (Plate 1, fig. G.)

Gemmill gives a diagram which illustrates the extremely modified curvature still recognizable in the adult asterid food-canal and its relation to the food-canal of the larva. This diagram shows very well the migration of the mouth to a central position on what was the original left side of the larva, and is now the ventral surface, with a corresponding migration of the anus to the new oral surface.

2. At this stage there was an acute divergence in the way of feeding (MacBride, [9], p. 563, and Gemmill, [5], p. 265).

One branch, the Crinoidea, make use of the functional activities of the stalk to raise the theca from the bottom and turn the tentacle-bearing surface until it faces the sea-surface.

The skeleton of the second branch (the Eleutherozoa) develops quite differently. The tentacles themselves spread along grooves arising from the stomodaeum. A new skeleton floors this groove. It consists of a double series of plates (the ambulacral plates) each pair of which is associated with a tentacle. Around the mouth this new skeleton comes into intimate association with the old stomodaeal skeleton.

Further differentiation in the Eleutherozoa is intimately associated with the varied use of the new skeleton in association with the old skeleton.

Two main branches arise: the Asterozoa and the Echinozoa. The Asterozoa (the Asteroidea and the Ophiuroidea) make very considerable use of the new skeleton, which becomes carried outward on angular growths from the original theca. In the Ophiuroids, as the extreme case, the new skeleton becomes the main skeleton of the animal.

The Echinozoa, on the other hand, ignore the possibilities of the new skeleton which, except in the immediate mouth region, becomes very early incorporated into the general thecal skeleton. In the extreme case—the Holothurioidea—a skeleton is almost entirely discarded.

On the other hand, the Echinoidea (and probably the early Holothurioidea (MacBride and Spencer [10], pp. 122, 132)) take on a new use for the old skeleton. The stomodaeal valves, by association with oral elements of the new skeleton, become adapted first as mud scoops, later as biting teeth.

The final result is that we have the Asterozoa, wanderers, hunters of flesh; Echinoidea which so often return to the phytal zone; Holothurioidea, frequent inhabitants of the bottom; and Crinoidea feeding from the food shower. Whatever food there is in the sea, becomes available to the Echinoderm world.

Suggested new Classification.

It is suggested that the present sub-division of the Echinodermata into Pelmatozoa and Eleutherozoa be replaced by a new sub-division, the Dactylozoa and the Podozoa. The Podozoa are the Echinodermata with tentacles, namely the Crinoidea,

the Asterozoa, the Echinozoa, and the Holothurioidea together with the extinct Carpoidea (*sensu stricto*). The Dactylozoa had no tube feet but collected their food by ciliary currents which were created on long thin projections from the body for which we can use the term 'fingers' or 'brachioles' as differentiating them from the 'arms' or 'brachia' of the Crinoidea. These Echinodermata are the Cystoidea, the Blastoidea, the Edrioasteroidea, and *Dendrocystis* and its relations.

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PLATE I. GYROCYSTIS

(A 'Podozoan' or 'tentacle feeder' which apparently could change its shape).

A. The specimen is nearly perfect except for a portion of the upper skin. The pitted operculum and its girdle of stout plates are at the oro-anal pole. The operculum is closed.

B. Reconstruction showing the relationship of the intestine and tentacles to the skeleton.

C. Early stage in a developing Crinoid (*Antedon*). (After Seeliger.)

D. Front view of a specimen showing the operculum slightly open.

E. F. show extremes of the shape changes. The operculum in F. seems to have fallen backwards (towards stalk) before preservation. *an*, anus; *hrc*, hydrocoel ring at base of tentacles; *m*, mouth; *o*, operculum; *st*, stomodaeum; *t*, tentacles; *v*, oral valves; numbering of marginalia is after Jaekel. Number 5 on the right of figure D and on the left of figure F should read 5_1.

G. Diagram showing shift of mouth and anus from marginal to abanal and ventral positions in a developing starfish (after Gemmill); *m*, larval mouth; *M*, adult mouth; *A*, larval anus; *a*, adult anus.

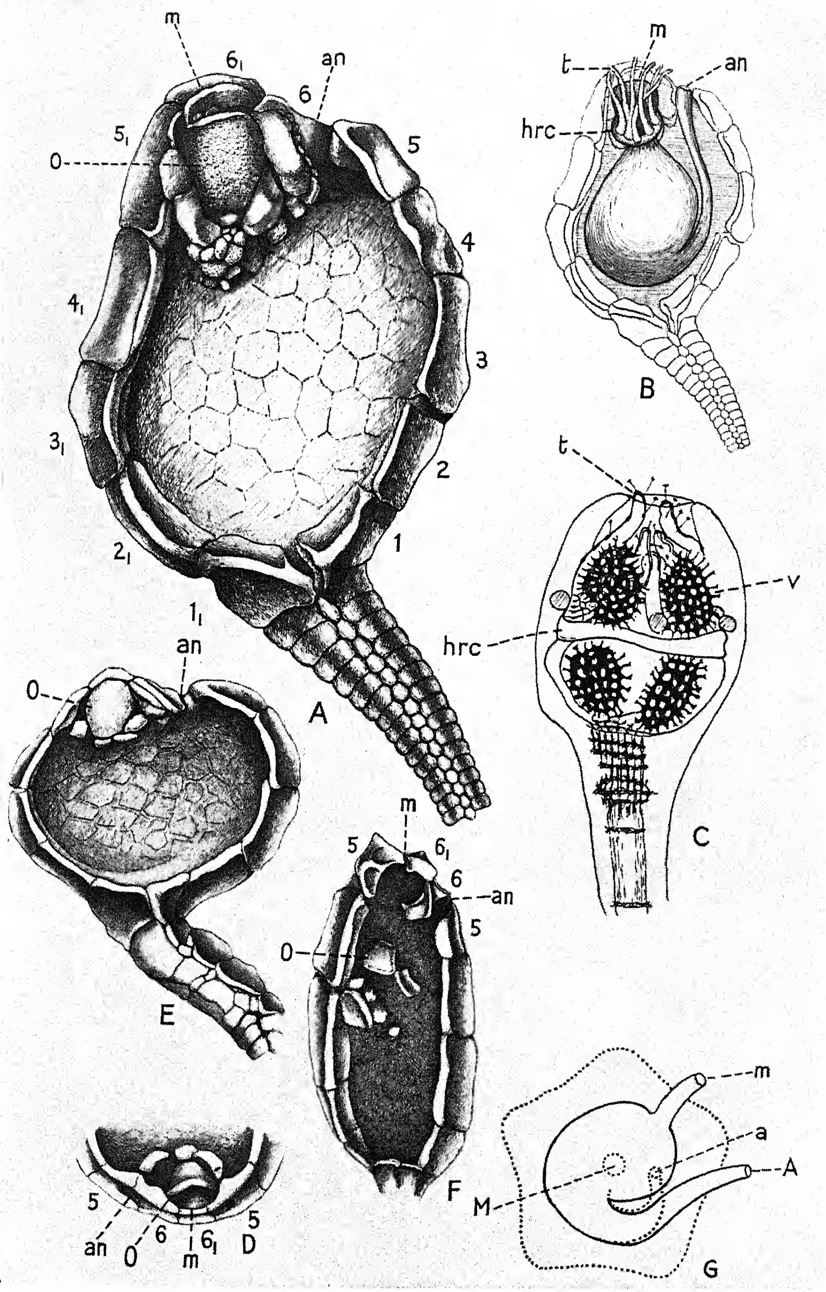
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PLATE II

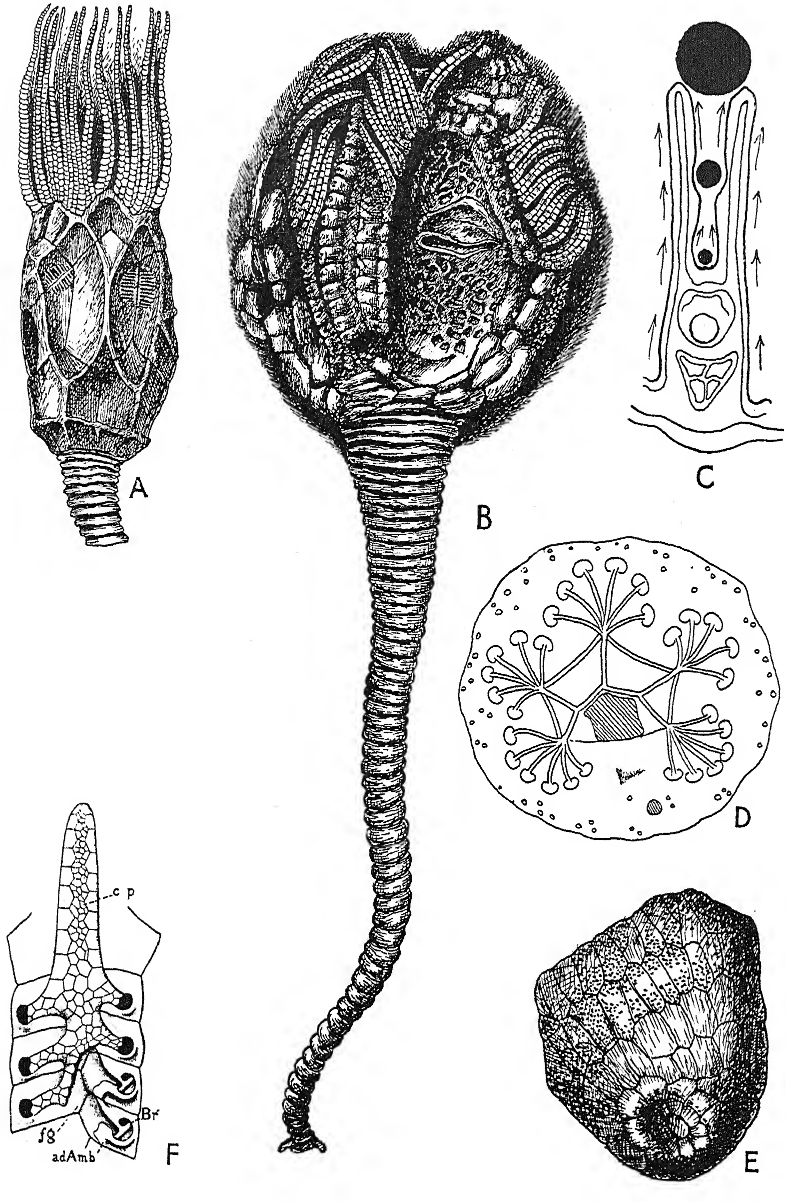

PLATE II. WHIRLERS (Dactylozoa)

A. *Cheirocrinus*. A Cystid showing the brachioles concentrated on the upper part of the theca. The mouth is within the circlet of brachioles. (After Jaekel.)

B. *Lepadocrinus*. A Cystid showing the brachioles spread in portions of great circles over the surface of the theca.

C. A diagrammatic transverse section through a pair of basal folds of the gills of *Sabella* to show the separation of particles by size. The large particles at the top are thrown out of the folds and discarded. (After Nicol.)

D. Hydrophores palmées of Barrande. The drawing shows the upper part of the theca of a Cystid (? *Craterina*) with narrow grooves radiating from a central mouth. The circular pits at the ends of the grooves were for the attachment of the brachioles which presumably formed a circlet as in *Cheirocrinus*. (After Barrande.)

E. The base of the theca of *Aristocystis* showing the beginning of the development of a stem as an extension of the thecal plates. A distinct sucker is carried on the distal extremity.

F. A portion of the adoral end of the food tubes of the Cystid *Mesites* slightly reconstructed to show the upper area of small plates, the hollow of the tube, the attachment of the brachioles, and the small side grooves running from the base of the brachioles into the main channel of the tube. (After Bather, modified from Jaekel.) *fg*, the groove carried on alternately arranged plates *adAmb*. *cp*, covering plates of the groove. *Br*, sockets for the brachioles.

THE PROBLEM OF THE EVOLUTION OF THE DERMAL BONES IN FISHES

By J. A. MOY-THOMAS

THE problem of the evolution of the dermal bones of the skull of Osteichthyes, and the comparison of them in the various groups of these fishes and with the early Tetrapods, is one which in recent years has attracted many workers in Vertebrate Palaeontology among whom may be mentioned Goodrich [4], Watson [20], Stensiö [17, 18], Nielsen [12], Säve-Söderbergh [15], Romer [14], Forster-Cooper [3], Allis [1], Westoll [21, 22, 23], and myself [9]. Unfortunately very little agreement has been reached by these writers, and in some cases the interpretations are mutually contradictory in almost every respect. The result of this has been a stalemate in which individual workers, refusing to accept the views of others, have persisted in their own. Much of this disagreement lies fundamentally in the very different ways in which each worker approaches the problem, and it is the object of this essay to examine the whole question afresh, not with the intention of providing a new theory of the homology of these bones, but with the intention of stating the problem in such a way that some agreement may eventually be reached.

The tendency among morphologists at the present time is to believe that the fundamental problems of their science lie more in determining the processes underlying the organization of animals rather than in providing further evidence for the now generally accepted theory of evolution by the production of more and more complete phylogenies. The morphologist should consider the developmental processes that have contributed to the formation of the adult, and not be content merely to compare the resulting forms without reference to these. The dermal bones of the skull of the Osteichthyes, like all other parts of the body, are dependent for their final adult shapes and arrangement on a number of different developmental processes. Therefore no comparison of the dermal bones is justified without first considering what is known of the causes of their development.

Unfortunately, it may be said at once that only very little is known for certain of the factors governing the development of bones in fishes, and what is known is mainly of an inductive rather than an experimental nature. The development of the bones of fishes has been to a very great extent a neglected field for experimental research; and it is a significant fact that Murray [10] in his book dealing with the causal development of bones nowhere mentions fishes. Although in higher animals many outstanding problems remain to be solved, a certain amount is known. It appears that in these forms the determination of individual bones is to a great extent laid down early in development, their final shapes only being determined by the stresses and strains of later development. This does not seem to be entirely the case in fishes, and it is due to workers assuming that the dermal bones of fishes are formed in this way that much of the controversy of their homologies exists.

Embryologists are in general agreement that the sense organs (neuromasts) of the lateral-line canal system play a very important part in the ontogeny of the dermal bones of the skull in fishes. The now classical account of the development of the skull of *Amia calva* by Pehrson [13] has shown that many of the dermal bones start their development as aggregations of osteoblasts round certain of these sense organs, forming small rudiments of bone which may or may not fuse with adjacent rudiments to form the adult bones, through which the sensory canals pass. On the other hand, those surface organs which never develop beyond superficial pit-lines appear to have little effect on bone development. The result of this is to produce a series of small ossifications along the sensory canals very early in development, the majority of bones, which in the adult are unconnected with the canals, developing later. Of the latter, the tooth-bearing bones and those of the opercular apparatus tend to be formed early. Each tooth is primarily underlain by a rudiment of bone which fuses with neighbouring rudiments to form the adult bones (Moy-Thomas [8]), and the functioning opercular apparatus early acquires bony support.

Thus the lateral-line sense organs and the early developing teeth may be said to be responsible for the precocious localization of bone-formation in their vicinity, the former producing series of ossifications along the canals. However, neither the

sense organs nor the teeth control the sutures between the adjacent bones. This may be demonstrated by the extraordinary variability of the adult bones in certain sensory canal series in the same species and even on different sides of the head of the same individual. Such is the case of the bones developed in connexion with the infra-orbital canal in *Amia calva*. The 'normal' or at least most frequently found condition is the one described by Pehrson in which two post-orbitals, two infra-orbitals, and a lacrimal are developed (Fig. 1 *A*), the dorsal post-orbital being formed in connexion with one, the ventral post-orbital with two, each infra-orbital with one, and the lacrimal with two sense organs. In some (Fig. 1 *B*, *C*), however there is only a single post-orbital, which may vary in size, whereas in others (Fig. 1 *C*, *D*) there may be a single infra-orbital also varying in size. Numerous other variations occur in addition to these. All these can easily be explained by assuming that the individual rudiments formed around the sense organs have become fused with one another in different combinations, as indicated in the Figures. Thus, for example, a single post-orbital of the types figured in Fig. 1 *B*, *D*, or two as in Fig. 1 *A* are produced. Nothing is known of the causes of these different fusions, or what is responsible for the limits of individual bones.

However, the bones in some canal series are far more constant in their limits than those in others. For example, the supra-temporal, post-frontal, frontals, and nasals do not, as far as I know, vary in *Amia*. It should be noticed that there is one difference of importance between these bones and the infra-orbital series. In the latter the bones are not connected with underlying bony structures, whereas in the former they form to a great extent the roof of the neurocranium. The stability of development seems to be associated with the relative importance of the bones in the architecture of the skull, but here again there is no exact evidence as to the cause of the limitations of bones even in a stable series.

An interesting case, demonstrating that the relative importance of a dermal bone in the skull architecture influences to a large degree its final form, is found in the least specialized flat-fish *Psettodes belcheri*. In a normal Teleost, the infra-orbital series consists of a number of bones, usually about six, but in

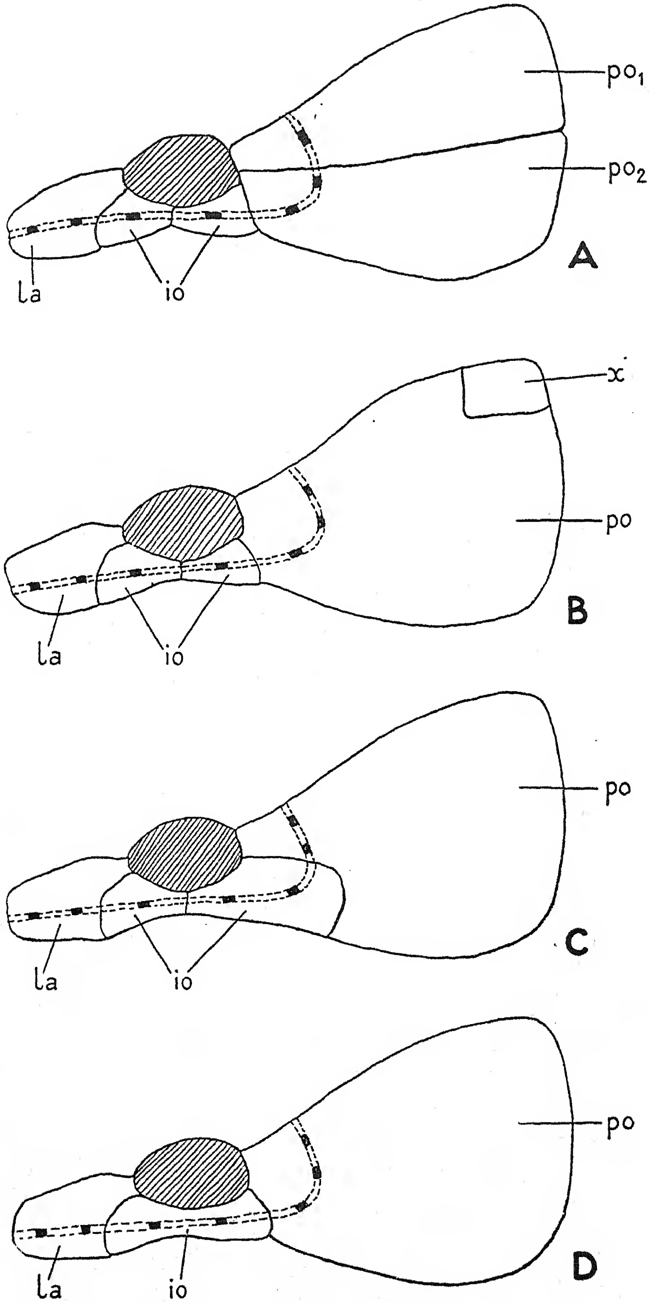

FIG. 1. For description see p. 309 below.

flat-fishes on the side of the migrated eye, they are more numerous and small, little more than tubules surrounding the canal. However, Chabanaud [2] has shown that in *Psettodes*, in which the twisting of the head is less complete than in other flat-fishes, the entire infra-orbital series develops as a single bone. This bone occupies an important position in the architecture of the skull, developing in the place of the new connexion, characteristic of other flat-fishes, between the frontal and pre-frontal of the side of the migrated eye. This connexion is presumably developed to give the twisted neurocranium more strength. In the majority of flat-fishes the twisting is too great for the bones developed on the infra-orbital canal series, which normally lie in this position, to play any part in its formation, whereas in *Psettodes* the twisting has not proceeded so far, the connexion being formed by the infra-orbital. This indicates very forcibly that the structural importance of a bone is correlated with its mode of development.

The nature of the development of the bones unconnected with the sensory canals, in so far as the processes which determine their boundaries and number are concerned, is unknown in detail. As in the case of the sensory-canal bones, in certain areas of the skull they are far more constant than in others. This is usually correlated with the size of the bones, which, in its turn, is probably correlated with the nature of the structures underlying them. In the sturgeons the development of the post-rostrals varies in almost every individual, and moreover Westoll [21] has demonstrated a similar variability in the post-rostrals of *Osteolepis*. In both these cases the bones concerned are relatively small, but in other regions such as the parietals in *Amia* and *Osteolepis* there is a tendency for larger bones to be developed. These bones are not entirely constant since rarely in *Amia* a single median parietal is found and in *Osteolepis*, although the majority of skulls have two parietals, many variations exist in which smaller and more irregular little bones are found. In the latter case, however, unlike the ethmoid region there is always a tendency for large paired ossifications

FIG. 1. *Amia calva*. Diagrams of the variations in the ossifications on the infra-orbital canal. The canal is represented by broken lines and the presumed position of the sense organs by the blackened areas on the canals. io = infra-orbital; la = lacrimal; po = post-orbital; po 1 = dorsal post-orbital; po 2 = ventral post-orbital; x = ossification of part of the post-orbital independently of the canal.

to be formed. No causal explanation of these variations can be offered. A further mystery may be cited in the case of the superior post-orbital of *Amia* (Fig. 1 *B*) which occasionally develops as a lateral-line bone but also in part as a separate ossification. Can this be explained as a reversion to the ancestral condition where numerous small bones (sub-orbitals) lay between the infra-orbital and pre-opercular canals? In other words, is it possible that the process responsible for the formation of sub-orbitals is still retained in some individuals of *Amia*?

There is some evidence of rather an unsatisfactory nature that the presence or absence of a bone is determined very early in development. The 'pug-nose' condition in Teleosts (usually caused by the failure of the pre-maxillary to develop properly) was shown by Knauthe [6, 7] probably to be inherited in *Leucaspis delineatus*.

Regeneration experiments by Tatarko [19] in *Cyprinus carpio* are of particular interest, since they show that in so far as the adult fish is concerned the limits of the bones of the opercular apparatus are not fixed, and a bone may come to occupy a considerably larger area after regeneration than before. For example, removal of the sub-opercular led to its place being filled by growth partly from the opercular and partly from the inter-opercular.

Since there is no doubt that dermal bones of the skull are comparable structures to the body scales, it is not surprising to find that the little that is known of their development shows similar processes and problems. Neave [11] has demonstrated, for example, that in the trout the scales along the trunk lateral-line canals are each developed in ontogeny in relation to a single sense organ. Nevertheless, nothing is understood of the processes which limit the development of the individual scales dorsally and ventrally, nor, for that matter, of what prevents the original canal rudiments from fusing with one another laterally, though the flexibility required of the trunk in connexion with the swimming movements probably plays a part.

The foregoing account of the processes of bone development may be summarized by saying that the sense organs of the lateral-line canal and the teeth are both responsible for the early development of bone in their immediate surroundings.

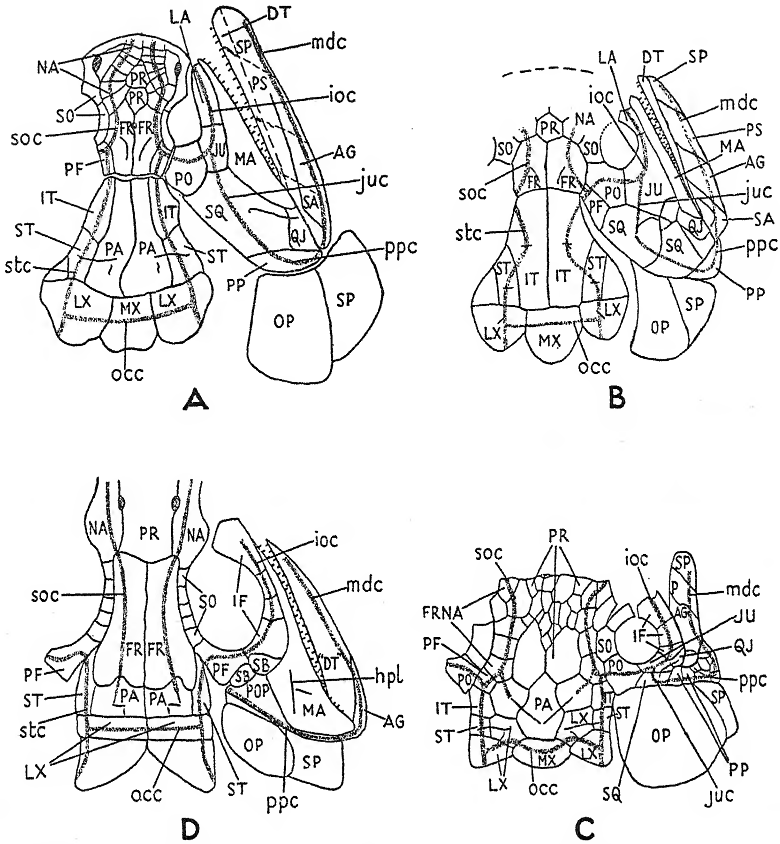

FIG. 2. Restorations of the skull roof and cheek of A. *Osteolepis macrolepidotus*, after Westoll, B. *Holoptychius flemingi*, after Westoll, C. *Dipterus valenciennesi*, after Westoll, D. *Elonichthys serratus* (the pit lines of the cheek are drawn from other fishes).

SO = supra-orbital
AG = angular
DT = dentary
'DT' = so-called dentary in Actinopterygians
FR = frontal
FRNA = frontal-nasal series of bones
IF = infra-orbitals
IT = inter-temporal
JU = jugal
LA = lacrimal
LX = lateral extrascapular
MA = maxillary
MX = median extrascapular
NA = nasal
OP = opercular
PA = parietal
PF = post-frontal
PO = post-orbital
PP, POP = pre-opercular
PR = post-rostrals
PS = post-splenial
QJ = quadrato-jugal
SA = supra-angular
SB = sub-orbital
SP = splenial (in lower jaw) = sub-opercular (in cheek)
SQ = squamosal
ST = supra-temporal
hpl = horizontal pit line
ioc = infra-orbital canal
juc = jugal canal
mdc = mandibular canal
occ = occipital commissure
ppc = pre-opercular canal
soc = supra-orbital canal
stc = supra-temporal canal

Since, however, the former lie along the canals which are arranged in a definite pattern on the head and in a somewhat similar manner in all Osteichthyes, they must play an im-

portant part in influencing the final arrangement of the bones. Corroboration of this may be inferred from cases where the pattern of the canals differs owing to the presence or absence of a canal, such as the jugal canal in Actinopterygians and Crossopterygians. As is to be expected, the development of the cheek bones is different in the two groups. In the Crossopterygii (Fig. 2 *A*, *B*) the jugal canal crosses the cheek transversely from the infra-orbital canal joining the pre-opercular canal, whereas in the Actinopterygii (Fig. 2 *C*) the pre-opercular canal runs down from the supra-temporal canal, the jugal canal being represented only by the horizontal pit-line. Consequently the early centres of ossification of the canal bones are in relatively different places in the two groups. The upshot of this is that the 'squamosal' ossifications of the jugal canal are not found in the Actinopterygii. The canals impart a symmetry to the skull but are not responsible for the limits of individual bones along them nor for their lateral boundaries. These vary considerably but must in some way be correlated with position and structural importance of the bones in the skull. It should, however, be noticed that to a certain extent the boundaries are indirectly limited by the canals. For instance, it is possible for an unpaired bone to develop on the roof of the skull between the supra-orbital or supra-temporal canals. The paired nature of the canals would prevent such an ossification being a canal bone. The formative stimuli of the bones unconnected with the canals can only be conjectured. The teeth in some way seem to be influential, but as in the case of the lateral-line bones and the dermal bones of Tetrapods, their development is to some extent regulated by the stresses and strains of development. There is no evidence concerning the causes of the start of their ossification, or the reason why the entire skull-roof, for example, is not covered with canal bones.

Since the lateral-line canal can only be assumed to provide the dermal bones of the skull of fishes with a general symmetry, and since the mechanisms which determine the limits of these bones are only imperfectly understood, it is hardly astonishing to find a great variability in different fishes, probably connected with their relative importance in the composition of the skull. It is on account of the essentially 'fluid' nature of these bones in fish that difficulties of making comparisons arise. The fish

skull cannot be considered in exactly the same way as the Tetrapod skull, where bone development has become a much more regular matter. It is because of this fundamental difference that confusion has arisen, workers tending to regard both skulls in the same manner. This may be illustrated by a few examples.

In *Polypterus* the area normally covered in other Actinopterygians by the supra-temporals and parietals is covered only by a pair of bones developed in connexion with the supra-temporal canals. The question has arisen, are these bones the supra-temporals? Are they the parietals which have become secondarily connected with the sensory canals? Or do they represent the fusion of the supra-temporals and parietals?

In *Amia* there is on each side a single nasal bone between the ethmoid commissure and the frontal, whereas in *Polypterus* there are three such bones. The nasals of *Amia* develop from three rudiments round three sense organs, those of *Polypterus* each from a single organ. Are those of *Amia*, therefore, the product of fusion or are the bones of *Polypterus* the results of fragmentation? These are just two examples from a great many more similar ones on which opinion is divided. Unfortunately, the trouble does not end with the acceptance or rejection of one of these possibilities. In each case the bone nomenclature is different, and those authors who believe in fusion have produced in some cases compound names which are so unwieldy that they defeat the very purposes for which bone names are coined. It is no convenience to use such terms as 'parieto-dermosphenopterotico-extrascapular', 'premaxillo-rostro-inter-rostro-nasal', or 'supra-orbito-supra-post-orbito-membrano-sphenotic'.

None of the possibilities outlined in the questions above seems really to be the correct solution, for all of them start with the assumption that there is such a thing as an easily definable 'bone'. What does one mean when one says 'the supra-temporal and parietal of *Polypterus* are fused'? What is the definition of a 'parietal' or a 'supra-temporal'? Sometimes this is answered with reference to the rudiments from which a bone develops. This increases rather than simplifies the difficulty by introducing the further question, whether all rudiments should be considered to be of the same value. In other words, what is 'a bone rudiment'? For example, are the rudiments that occur round

the sense organs equivalent to those that are found at the bases of the teeth? If the infra-orbital series of ossifications of *Amia* is considered (Fig. 1), it will be at once apparent that it is not possible to say whether a bone is either a post-orbital or an infra-orbital; the bones can only be defined in terms of what is believed to have happened during their development. A nomenclature of the individual bones in this case would only be an unnecessary hindrance, since they may differ on the two sides of the same skull. These bones must simply be considered to be a 'series'. It seems, therefore, that the only practical definition of 'a bone' in fishes is one which considers a bone to be a structure which can be dissected out as a separate entity in the adult. There is no reason to believe that a bone is necessarily exactly equivalent in size or development even in the same species. Such terms then as 'parietal' and 'nasal' cannot be intended to be exact, but simply approximations which will be useful for practical purposes. Such names must be used, otherwise it would be impossible to refer shortly, for descriptive purposes, to any individual ossification as has been done throughout this essay. This difficulty has been appreciated already by Forster-Cooper [3], who prefers the use of letters in *Dipterus* rather than bone names which imply doubtful or non-existent homologies.

However, since these bones of *Polypterus* are developed in connexion with the supra-temporal canal, they can therefore be more accurately compared with this series of bones in other fishes and may be considered to be supra-temporals.

Now, if this point of view be applied in making comparison of the dermal bones of the skull in the three chief groups of early Osteichthyes: the Crossopterygii, Dipnoi, and Actinopterygii, the result is not wholly satisfactory since there is so much that remains to be learnt about the processes of bone development, particularly as to the causes of ossification of non-canal bones. Nevertheless, a comparison of these types of skull in terms of what can be inferred of their development leaves the problem in a somewhat less confused state. For the sake of brevity this comparison is confined to the bones of the skull roof and cheek.

Osteolepis is one of the earlier Crossopterygians, and although there is considerable variation in pattern of the dermal bones in many specimens, Fig. 2 *B* represents a fairly characteristic

arrangement. On the skull roof it can be seen that the supra-temporal and supra-orbital lateral-line canals are continuous and joined behind by the occipital commissure. On this commissure three bones, the extrascapulars, are developed, and along each longitudinal canal a series of bones known as the supra-temporals, inter-temporals, post-frontals, frontals, and a number of small nasals anteriorly. The infra-orbital canal connects with this dorsal canal in the post-frontal and has the bones known as the post-orbital, jugal, and lacrimal developed on it; the jugal canal traverses the face backwards from the jugal with a single ossification, the squamosal on it, and joins the pre-opercular canal, on which is a single ossification, the pre-opercular, from whence the canal is continued forward again in the lower jaw, passing through four bones, the supra-angular, angular, post-splenial, and splenial. Lying between the anterior ossifications on the supra-orbital canal are a number of small bones, the post-rostrals, which are very variable indeed in different individuals (Westoll [21]). Between the supra-temporals two large ossifications, the parietals, are usually formed, which show some variations although they tend to be larger ossifications and less variable than the post-rostrals. Between the dorsal edge of the orbit and the supra-orbital canal lie two supra-orbitals, beneath the eye the long tooth-bearing maxillary and posteriorly the quadrato-jugal.

In the later, but closely allied, Crossopterygian *Holoptychius* (Fig. 2 *B*), the condition is slightly different. Firstly, the marked discontinuity of the neurocranium dividing the cranial roof into anterior and posterior moieties as in *Osteolepis* is not present. There are no separate ossifications between those on the supra-temporal canals, the anterior of which has developed as a larger bone meeting its fellow in the middle line. An ossification unconnected with the supra-temporal canal occurs laterally to the supra-temporals; these bones are sometimes but not always present in *Osteolepis*. In the cheek there are two ossifications on the jugal canal, the squamosals. A further difference is to be found in the quadrato-jugal region where three ossifications are developed instead of the single one of *Osteolepis*.

In the skull of the early Dipnoan *Dipterus* (Fig. 2 *C*) conditions appear at first sight to be very different. The canal system differs slightly from that of *Osteolepis* in having the anterior

pit-line developed in part as a canal. The occipital commissure has five ossifications, the extra-scapulars, on it; the supra-temporal canal has two, the supra-temporal and inter-temporal, and, at its junction with the supra-orbital canal, a post-frontal. There is one bone developed in connexion with the posterior end of the supra-orbital canal (anterior pit-line) and a series of small bones, which vary in number even on different sides of the same skull, are developed in connexion with its anterior part. None of these latter bones become large, meeting their fellow in the middle line to form the large 'frontals' of the Crossopterygii. Nevertheless, the whole series since it is developed in connexion with the supra-orbital canal can be generally compared with the frontals and nasals of other fishes. The bones of the cheek are somewhat similar to those of *Osteolepis*, but the number of canal ossifications on both the pre-opercular and infra-orbital canals is greater than in this form. The major differences of the skull lie in the bones not developed in connexion with the sensory canals. Firstly, there is no maxillary, its loss being correlated with the peculiar palatal dentition. Between the anterior part of the supra-orbital canals as in *Osteolepis* lie a number of small ossifications varying greatly in different fishes. Directly posteriorly to them there tend to be two large paired bones lying between the eyes, although in some varieties these bones are smaller. In certain later forms like *Scaumenacia* (Goodrich [4]) it is these bones which tend to become the large paired elements between the eyes, whereas in others like *Fleurantia* (Graham-Smith and Westoll [5]) the lateral-line bones in this region are large. Behind these paired bones a single median bone is invariably found.

In a typical early Actinopterygian like the Palaeoniscid *Elonichthys serratus*, the lateral-line canal system of the head differs in two respects. Firstly, the supra-orbital canal does not join the supra-temporal, and secondly, as already mentioned, the pre-opercular canal is connected with the supra-temporal, the jugal canal being represented only by a pit-line. There are only two extra-scapular ossifications, and a single ossification on the supra-temporal canal, the supra-temporal, in front of which the canal turns downwards under the eye as the infra-orbital canal. On this canal a number of ossifications are

formed, the infra-orbitals, the most dorsal usually being termed the post-frontal. Posteriorly, the supra-orbital canal arises in a pair of bones lying in the same region as the parietals of *Osteolepis*, anteriorly to which the larger frontals and nasals are developed on the canal. The post-rostral region is covered by a single bone. The cheek is modified from the *Osteolepis* pattern, due to the altered course of the pre-opercular canal. A single ossification, the pre-opercular, is formed on this canal, and only two are formed on it in the lower jaw. A number of small bones, the sub-orbitals, are formed between the infra-orbital and the pre-opercular canals, and there are five supra-orbital ossifications.

In making a comparison of these skulls, it seems to be a fairly just assumption that the skull was originally covered with a large number of small bones similar to the scales, and that each sense organ had a single one of these ossifications developed in connexion with it. These bones at first would play no very important part in the skull architecture, but as their significance in this respect increased in the course of evolution, the original small bones became superseded by larger areas of ossification. In fact, in each ontogeny the processes of development would change in various ways in different parts of the skull. Nevertheless, the sense organs on the lateral-line canal still influence the final pattern since they are to a great extent responsible for the precocious development of bone in their vicinity. Similarly, the tooth-bearing bones would be developed proportionally to the development of the teeth. If these developmental processes were similar in all three types of skull the resulting bones would also be similar, but this can obviously be seen not to have been the case since the arrangement of the bones and general shapes of the skulls in each form are very different.

The effect of this on the skull has been that there are a number of bones in each skull developed in 'series' along the canals, but the individual limits between bones are not by any means exactly comparable, nor are the areas covered by them. Since these 'series' are generally formed first in ontogeny, they are apt to be retained in phylogeny and to become more important at the expense of the other bones. In some regions of the roof there is a tendency for the development of

larger bones than in others. In certain fish it is the lateral-line ossifications which have become large and paired, for example the inter-temporals of *Holoptychius*, whereas in others such as *Osteolepis* this region is covered by bones unconnected with the canals, the parietals. One of the major problems of comparison is not, therefore, whether there have been fusions or dropping out of bones, but why the paired median bones were developed from the lateral-line ossification in *Holoptychius* and not in *Osteolepis*. Similarly, why do paired ossifications between the eyes in *Dipterus* tend to be non-lateral-line bones, whereas in all others they are lateral-line bones? If in one fish a region can be covered by canal bones, what prevents it being covered by them in another?

All these questions can only be answered with reference to the factors governing development, and the only exact comparisons can be made in these terms. Since so little is known of these processes, no exact comparisons are possible. Nevertheless, one is justified in comparing bones along a canal as a 'series' since they have all been developed in connexion with sense organs. The ossification, such as those termed the post-rostrals lying between the canals, can only be compared in so far as they cover approximately the same region and are not connected with the canals.

In conclusion it may be said that there is really very little point in trying to make exact comparisons between bones, where no such exactness exists. The use of bone names is valuable in so far as they are of practical use. If a comparison is to be made between *Dipterus* and *Osteolepis*, it is more useful to say that in each skull a certain number of ossifications are developed in connexion with the sensory canals, but that the other processes of development are so different in the two fishes that the number of bones and their final arrangement cannot be further compared, rather than to try and make exact comparisons between individual ossifications, which may vary considerably in the same species. Each fish shows a tendency for paired and larger bones to be developed in certain regions and irregular smaller ones in others, but the causes of their formation are as yet unknown, as are those for the limitations in size and consequently in number of any particular ossification in a 'series' along a canal.

It is, therefore, at present only possible to compare the ossifications along canals in early fishes. These fall into the occipital commissure series, the supra-temporal canal series, the infra-orbital canal series, the pre-opercular canal series, the jugal canal series, and the mandibular canal series. The number of ossifications in a series is too variable for individual homologies to be made. The remaining areas can be compared only as the post-rostral, the parietal, maxillary, and quadrato-jugal regions.

Only experimental evidence can solve the fundamental problem of the causes of the size of a bone, and the factors actually determining the start of bone formation. Such evidence may show that here too much emphasis has been laid on the bone-forming powers of the sensory canal organs, but at present they alone provide some clue to the processes of development in the dermal bones of fishes.

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FUNCTIONAL EVOLUTIONARY MORPHOLOGY: THE ORIGIN OF BIRDS

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IN attempting to reconstruct the early evolutionary history of many groups of animals a certain element of judicious speculation, provided that the conclusions are constantly checked and tested with reference to such fossil types as may be known and to such characters of modern forms as may have a bearing on the subject, may be a valuable weapon. It is only exceptionally that the fossil record of any group is complete enough to allow a direct reconstruction of the critical stages of its evolution in structural terms, while as regards the mode of life of ancestral forms and what may be called the biological aspects of the phylogenetic history, conclusions must necessarily be reached indirectly. Yet the rise of all the major groups of vertebrates has been intimately bound up with important functional changes, that of the fish with the first exploitation on a large scale of the whole chordate type of organization, of the amphibia with adaptation to air-breathing and terrestrial life, of the reptiles with the completion of emancipation from the water, of the birds with flight, and of the mammals with improvement in brain development and general functional efficiency. These biological aspects of phylogeny are thus fundamental to an understanding of the evolution of every group: an attempt to arrive at reliable conclusions with regard to them must go hand in hand with the study of structure, and indirect evidence must thus perforce play a considerable part in the reconstruction of any phylogenetic histories which are to get beyond a merely formal morphology and to regard the subjects as living and functioning organisms. There is no group in which an application of the methods of this kind of functional evolutionary morphology is more important than that of the birds, for here *par excellence* is a group whose whole organization was bound up in its origin with a functional change of far-reaching significance, the transition from terrestrial to aerial locomotion. It is proposed

to devote the present essay to a review of certain general problems of bird phylogeny on the lines indicated, the present time appearing particularly opportune for the purpose, both on account of the renewed prominence given in recent years to certain controversial aspects of the subject and of the negligible impression that various relevant matters of theory and fact published in the last twenty years seem to have made on the general literature of avian evolution.

The reptilian ancestry of birds is so self-evident and so universally recognized by zoologists that it can be taken as axiomatic in any discussion. We shall further accept the view that the immediate reptilian ancestors of birds, if known, would have to be placed in or extremely close to the group of Pseudosuchia. The direct derivation of birds from dinosaurs, favoured by some earlier writers, would probably not be advocated by any competent zoologist at the present day, but the many similarities between the two groups suggest a common origin. The Pseudosuchia probably comprised the ancestors of all the other Archosaurian reptiles, including both Saurischian and Ornithischian dinosaurs, and Broom [1] in particular has stressed the fact that such a Pseudosuchian as *Euparkeria* fulfils all the positive requirements of an avian ancestor, while lacking the specializations which exclude the dinosaurs from this position.

The problem of the evolutionary beginnings of the class Aves may be said to be synonymous with that of flight and feathers. Since any conclusions which may be reached in this connexion must be formulated with reference to the structure of the earliest known fossil birds, it may be desirable to recall briefly the main characters of the latter, notwithstanding that they are very generally known. Probably no single fossil type constitutes a more impressive demonstration of organic evolution, a fact which was not overlooked by Wagner, who in introducing *Archaeopteryx* to the scientific world in 1861, soon after the publication of the *Origin of Species*, felt obliged to 'add a few words to ward off Darwinian misinterpretations of our new Saurian'.

Archaeopteryx and *Archaeornis*, then, though indubitably birds, as witnessed by their well-developed and typical flight-feathers, their limbs, and indeed their whole skeletons, proclaim their

reptilian ancestry in no uncertain fashion. The Pseudosuchian-like skull and toothed jaws, the separate clawed digits of the hand, the long lizard-like tail, and the gastralia are all startlingly reptilian features. Yet in fact they are only what might be expected in the most ancient birds and in line with, though superficially more striking than, such other primitive features as the non-fusion of the metatarsals, the long vertebral column and amphicoelous vertebrae, the free cervical ribs, and the less consolidated, though quite avian, pelvis.

The classical theory that the 'Pro-avis' which formed the link between *Archaeopteryx* and the reptiles was an arboreal parachuting creature, which took flying leaps from tree to tree with its legs splayed out like a flying squirrel, has gained currency in this country chiefly through the writings of Pycraft, though it was clearly enunciated many years earlier by Marsh [11] and Fürbringer [6]. Pycraft [15] imagines a scaly creature in which the scales along the hinder aspect of the arm became 'frayed out' in adaptation to supporting the body in the air. These frayed-out scales are supposed to have been the progenitors of quill-feathers and subsequently (or concurrently) by a sort of secondary extension of the fraying-out tendency the scales of the rest of the body are assumed to have undergone a similar metamorphosis. We shall return to a further consideration of this idea at a later stage.

The arboreal theory of the origin of flight was the only serious competitor in the field[1] until Nopsca [12] in 1907 attacked it and put forward his theory of a cursorial Pro-avis, which he supported with additional arguments in a paper published in 1923 [13]. Nopsca stresses the admitted affinity of birds to dinosaurs, and maintains that the ancestral birds must have been bipedal. His main objections to the theory of a quadrupedal parachuting phase are that if birds only became bipedal secondarily after acquiring the power of flight, 'it is difficult to understand why they in general show dinosaurian affinities' and that a parachuting mechanism is impossible in a bipedal animal. He takes it for granted that

[1] It is unnecessary to treat seriously the grotesque theory that the ancestors of birds were aquatic and developed the wings for swimming. The fact that those modern birds whose wings are most specialized for swimming, namely the penguins, have lost the most characteristic organs of the wing, the quill feathers, should suffice to underline the absurdity of this idea.

'parachuting' implies a patagium, which in its turn requires an essentially quadrupedal habit, in which the hind limbs as well as the fore can be stretched out laterally in a fashion mechanically impossible in a type with limbs adapted to a bipedal carriage. If, on the other hand, the ancestral forms were quadrupedal the natural method of acquiring the power of flight would have been for them to develop a patagium, as all other quadrupedal flying animals have done, and this very development, by incapacitating the hind limbs for walking, as has happened in other quadrupedal fliers, e.g. bats and pterodactyls, would have precluded the subsequent development of bipedalism. Therefore, it is argued, the ancestral birds cannot have had a patagium, a conclusion which is further supported by the considerations that there is no obvious reason why a patagium which had once begun to develop should have ceased to do so, and that feathers developed on the edge of such a flexible membrane would have been mechanically useless. Nopsca therefore put forward a new conception of the 'Pro-avis' as a bipedal, running reptile which increased its speed by beating the air with its arms as it ran.

Nopsca's objections to any theory involving a patagium seem unanswerable, but his general argument is open to considerable objections. In the first place, the assumption that a stage of patagial gliding is a necessary part of the arboreal theory is not justified. In the second, there is the almost invariable rule that terrestrial bipedal animals undergo a marked reduction of the fore limbs. Yet the fore limb of a bird is rather long. Nopsca endeavoured to meet this obvious objection, brought forward by Hay [8] and others, by pointing to the case of the Cretaceous Saurischian dinosaur, *Struthiomimus*, which had longer arms than most bipedal forms. But the case is sufficiently exceptional at any rate to emphasize the need of caution, and Nopsca's view that the ancestors of birds did in fact reduce their fore limbs and subsequently enlarged them will not commend itself to most zoologists without much better evidence to support it. Another objection justly cited against Nopsca's theory was the possession by birds of a rotated and grasping hallux, which seems to be clearly an arboreal adaptation. Nopsca's reply to his critics was to demonstrate from footprints that a number of terrestrial reptiles of the Trias had

a more or less rotated hallux, but as this rotation was generally accompanied by reduction he had to suppose that a reduced hallux in the Pro-aves was secondarily enlarged into a functionally effective organ in their descendants. This was in line with his belief that the so-called 'Law' of Irreversibility of Evolution does not invariably hold good, but the assumption is one which it seems unwise to make in any particular instance without very strong evidence.

Again, it is a very general rule that terrestrial bipedal animals lose the clavicles, while arboreal forms require these structures to resist the lateral strain on the shoulder joint in climbing and jumping, and so preserve them. If the furculum of birds represents, as is usually supposed, the fused clavicles, this would be a very strong argument against a cursorial origin of the group. This was fully recognized by Nopsca, who maintained that no similar fusion of the clavicles occurred in any other known vertebrates and that the furculum was in fact an ossified tendon developed to resist the lateral strain in an arboreal animal amongst whose terrestrial ancestors the clavicles had been lost. This is a perfectly legitimate argument and the possibility cannot be excluded, but it is an insecure basis on which to found any far-reaching hypothesis. Moreover, contrary to Nopsca's assertion, the relations of the furculum with the adjacent bones appear to constitute no obstacle to the usual view of its homology.

It would be impossible here to examine Nopsca's theory at length, but sufficient has been said to show that it certainly does not solve all difficulties, as its author claimed. It is permissible to add a final consideration of a general biological kind. It is reasonable to suppose that most big evolutionary changes, like the acquisition of the power of flight, were encouraged and made possible by natural selection because even in their early stages they conferred some definite advantages. It is hard to believe that beating the arms in the air could have affected the speed of Nopsca's terrestrial Pro-aves so as to have been any use to the animals or to provide any incentive to the development of quills on the fore limbs. On the other hand, it is very easy to see that an arboreal animal which, by whatever mechanism, could take longer flying leaps from tree to tree than would otherwise have been possible, would have acquired

a very considerable advantage against both arboreal and terrestrial enemies. Moreover, even if we imagine the beginnings of wings to have been acquired on the ground, so that the owners could take gliding leaps through the air as they ran, it is quite incredible that any substantial advance could have been made towards the attainment of true flight without the creatures becoming arboreal, as, indeed, *Archaeopteryx* obviously was, and this is admitted even by supporters of the cursorial theory. It becomes desirable, therefore, to inquire whether there is really any good reason for supposing that they were not arboreal from the outset.

The writer is convinced that the solution of the whole difficulty is provided by regarding the ancestral form as an arboreal reptile with the hind legs modified for springing. From a careful consideration of all the data he had been led independently to this conclusion before discovering that the same idea had been most convincingly advocated by Steiner [16], as long ago as 1918, in connexion with his researches on the nature and origin of diastataxy.

Most of the known Pseudosuchians displayed a more or less marked tendency to enlargement of the hind limbs. Some of them had the fore limbs decidedly reduced and were perhaps genuinely bipedal to a considerable extent. Others may have reared up on their hind legs as they ran, like the modern frilled lizard (*Chlamydosaurus*). But it may well be supposed that bipedalism in Pseudosuchians and their descendants, the dinosaurs, was the sequel to an enlargement of the hind limbs which took place in the first instance in adaptation to leaping, in early types which were still essentially quadrupedal. Steiner imagines the Pro-avis as a small, generalized, arboreal Pseudosuchian somewhat like the modern Agamid lizards in form, in which the springing habit led to an enlargement of the hind limbs and elongation of the metatarsals. The fore limbs, being used in climbing and in steadying the body after a leap, did not become reduced, as in bipedal terrestrial forms. The position of the hind limbs in springing, as well as the general activity of the animal's movements, precluded the formation of a patagium, but instead the precursors of quill feathers developed along the hinder aspect of the arms and the sides of the tail, tending to buoy up the body in the air in essentially the same manner.

Steiner has maintained that the reduction of the ulnar digits, as seen in the bird's hand, is a typically arboreal adaptation, since in maintaining the equilibrium of the body in climbing up branches most work would be thrown on the inner digits. Nopsca has disputed this, but if Steiner's evidence is less conclusive than he supposed, his arguments in the main appear well founded, as applied to animals climbing by the aid of sharp claws instead of grasping. On the other hand, Nopsca's objections to the theory of a springing Pro-avis from analogy with *Tarsius*, *Galago*, or frogs appears to overlook an important point. He insists that all these forms elongate the tarsals and not the metatarsals, it being essential in jumping animals 'that that part of the pes should be rigid and long which immediately touches the tibia and not the part beyond the flexible tarsal bones'. This argument, however, seems to ignore the fact that while the ankle joint is tibio-tarsal in mammals it is inter-tarsal in reptiles. In the latter the proximal tarsals plus the tibia form a functional unit and the distal tarsals plus the metatarsals another, with the line of mobility between them, and in such animals the saltatorial adaptation referred to by Nopsca would be expected to take the form of an elongation of the tarso-metatarsus as a whole.

At first the hand must have remained free, but as the primitive quill feathers grew larger and the length of the previously passive gliding flights began to be extended by an active beating of the air with the wings, the point where the supporting power was most needed shifted outwards and the primary quills arose on the hand. The gradual transformation of the arm into a wing was accompanied, in Steiner's view, by the gradual assumption of a bipedal carriage; the hallux, which in the lizard-like stage became turned inwards at something like a right angle to the others, to resist the tendency of the body to slip off on one side or the other of the cylindrical branches, became further rotated into the definitive avian position and the foot assumed the grasping function which it has in *Archaeopteryx* and modern birds. Bipedalism in birds and dinosaurs was thus an example of parallelism or convergence from a quadrupedal ancestor, the enlargement of whose hind limbs in adaptation to springing no doubt constituted a predisposition to bipedal carriage. But while the dinosaurs on the ground perhaps began

to acquire a cursorial type of bipedalism before the springing adaptation as such had developed very far, the Pro-aves accentuated the springing habit and only later became fully bipedal.

What is in effect a variant of Steiner's theory has been advocated by Böker [2, 3, 4], who maintains that there never was any phase of passive gliding, but that from the outset the avian ancestor must have made flapping movements with its arms during its leaps. He is led to this conclusion by an extensive study of the relative lengths of the segments of the fore limb in modern birds, in which he finds a close correlation between these proportions and the type of flight. He further believes that bipedalism, though developed in connexion with springing habits in trees and not on the ground, was acquired at an earlier stage than supposed by Steiner. His investigations lead him to postulate the following evolutionary stages: (1) Tree-climbing reptile of lizard-like form; climbing and quadrupedal springing in branches. (2) Bipedal springing, but hands still used in alighting and in climbing. (3) 'Pro-avis'; as last, but springing combined with flapping movements; attainment of permanent bipedalism almost completed. (4) *Archaeopteryx* stage; fluttering leaps, beginning of flapping flight, combined with gliding, permanent bipedalism, gripping function of hand preserved. (5) True flight, at first flapping, not long sustained, with little lifting power, and much gliding.

The limb proportions in *Archaeopteryx*, according to this author, indicate a laborious flapping action something like that of the poorer fliers amongst the living game-birds, though no doubt with even less lifting power and incapable of being long sustained. There seems much to be said for Böker's views, which are the result of a careful and critical study, but the difference of his standpoint from Steiner's is not fundamental. If the stages at which arm movements began and an upright carriage was assumed are still debatable, there is full agreement in the essential conception of the Pro-avis as neither a quadrupedal parachuting glider nor a terrestrial bipedal runner, but an arboreal springing reptile, and this view of the matter appears so much more satisfactory than the alternative theories that, in the submission of the writer, it is quite time it was more generally recognized as much the most likely, if not in fact the only workable, hypothesis.

Steiner accounts for the phylogenetic origin of diastataxy in an ingenious manner. His researches demonstrate conclusively that the apparent absence of the fifth secondary quill in diastataxic forms is due to a dislocation of the feather rows at the level where the diastataxic gap occurs,[1] while the absence of any such gap in eutaxic forms and the apparently regular

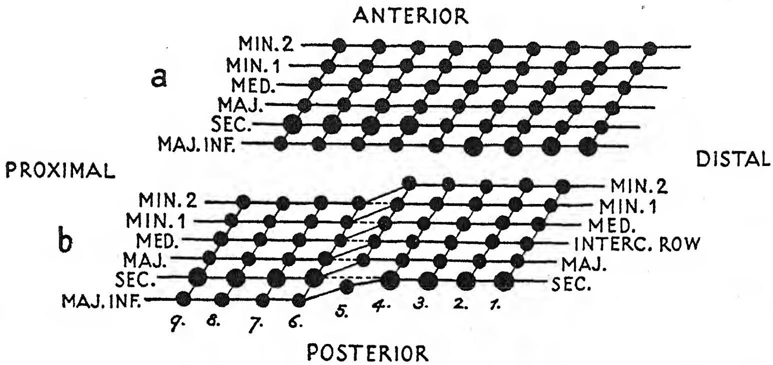

FIG. 1. Steiner's diagram illustrating the origin of Diastataxy: *a*, before, and *b*, after the dislocation. In *b* transverse rows 1 to 5 have been displaced upwards. Nos. 1–4 of the original horizontal row of inferior major coverts come into line with the proximal members of the secondary row and themselves become secondary quills, but No. 5 is just in the transition region and does not become a quill; hence the gap in the series of secondaries. A point which the diagram does not make clear is that towards the anterior border of the arm the upward displacement of the rows must be supposed gradually to lessen so that the more anterior (upper) rows are not (or scarcely) affected, the lower rows being, in fact, not merely 'faulted' upwards, as shown, but squeezed together to some extent. Consequently in the distal part of the wing there is one more horizontal row of coverts than in the proximal part, the so-called intercalary row of diastataxic wings being thus accounted for.

correspondence of coverts and quills in the latter are due to a secondary readjustment, diastataxy being the more primitive condition. Steiner relates the origin of this dislocation in phylogeny to the altered mode of flexure of the hand at the wrist joint. In typical vertebrates the movement of the hand is mainly up and down. But in the closed wing of a bird the hand is folded sideways towards the ulna through an angle of nearly 180°. The development of this new type of flexure in

[1] It is to the credit of Pycraft [14] that he was the first to recognize that diastataxy was due to such a dislocation or 'faulting' of the feather rows, but owing to inadequate embryological material he was led to suppose that the distal portions of the rows were displaced downwards, whereas Steiner's exhaustive investigations show conclusively that the reverse occurs.

the ancestral bird must necessarily have affected the incipient feathers lying in the angle, which are supposed by Steiner to have been pushed out of place by this new type of hand movement. The fact that just 4–5 rows were involved in the displacement was presumably merely accidental and dependent on the fact that the compression of the integument resulting from the new movement would extend for a certain distance only. In consequence the more proximal palaeoptiles, if it is permissible to coin a new term,[1] retained their original position. As subsequently, with the perfecting of the power of flight, the palaeoptiles became better developed, those of one horizontal row came to form a continuous series with the 4–5 distal members which belonged before the dislocation to the row below, and those nearest the post-axial border—that is in the position of greatest functional importance—underwent their final modification into true quills. But the fifth transverse row was just in the transitional region between the upper distal and the lower proximal halves of the original horizontal row, so that in it no quill was formed. This is the only reasonable phylogenetic explanation of diastataxy that has been put forward, and if it should appear at first sight of a rather Lamarckian colour, it must be insisted that it is just as capable of being visualized in Darwinian terms as any other adaptive change.

Up to the present the problem of the origin of feathers has been deliberately left on one side, and this must now be considered. In recent years the idea which seems to have been most generally adopted is that of Pycraft, who, as previously mentioned, supposed that feathers were the result of a 'fraying out' of scales (the precise nature of this process being unexplained), which began adaptively on the arms and spread to the rest of the body. This theory was somewhat uncritically copied by one writer after another mostly without any attempt to explain how the transformation of a scale into so strikingly different a structure as a feather might be supposed to have occurred or to meet the obvious difficulty that frayed-out scales would have been useless as supports without the complex interlocking mechanism which distinguishes the feather and which can hardly have been developed all at once. Ewart [5] has

[1] By this term is meant the ancestral forerunners of the definitive feathers whether they are supposed to have been derived from scales (cf. p. 332) or not.

already criticized the idea of the intimate phylogenetic connexion of feathers with scales, and the writer has long felt that a feather covering of a simple sort is much more likely to have arisen as an insulating device in non-flying ancestors which were becoming 'warm-blooded' than in the manner suggested by Pycraft. This view of the origin of feathers was in fact widely held by earlier writers, such as Fürbringer [6] and Wiedersheim, and seems to have been rather lost sight of in recent years. If we suppose that a general covering of epidermal processes having somewhat the structure of coarse down feathers (and perhaps developed between the scales, as hairs apparently were) existed before the first phylogenetic experiments towards 'learning' to fly, and further that the finer processes already tended to interlock to some extent, it is very much easier to imagine those on the arm undergoing an adaptive enlargement than to postulate the development of quills *ab initio* at this stage. Such a view need not entail assigning any phylogenetic significance to the down feathers of the nestling. It seems necessary to emphasize that even from the modern view-point on recapitulation, as advocated by Garstang and de Beer, there appears no *theoretical* objection to regarding such structures as recapitulatory in an indirect sense. For supposing that in a primitive member of a group the characters of young and adult were not very different, ontogenetic features of later forms, although strictly to be regarded as corresponding to ontogenetic and not adult ancestral stages, may still afford a valid clue as to what the latter were like. But in actual fact it is very doubtful whether down feathers can be regarded as 'recapitulatory' in even this indirect way. In recent years the view has gained ground that the nestling down feathers are not a separate 'generation' of feathers at all, but merely the precociously developed, fluffy tips of the definitive feathers, since they form from the same papilla and the shaft of the neossoptile is in direct organic continuity with the rami of the teleoptile. In these circumstances it may well be questioned whether the nestling down has any phylogenetic significance whatever, but it can still be argued on general grounds that the palaeoptiles are likely to have resembled the simple down feathers in structure more than the complex definitive feathers.

The writer still feels that such considerations have

considerable force, but, on the other hand, Steiner has made out so much better and more detailed a case than previous writers for the essentially primitive character of the quills and their direct derivation from scales that his views deserve to be most carefully considered.

Steiner argues at some length against the phylogenetic significance of down feathers, emphasizing the organic continuity of the neossoptiles with the teleoptiles and maintaining that various features occurring in down feathers, such as the occasional presence of hook processes (hamuli), can only be regarded as non-functional relicts, derived from a type of feather adapted to flight. In accordance with what has been said above it may be observed that this may mean no more than that the present-day down feathers are *not* primitive, and need not affect the question of what the palaeoptiles were like. He further directs attention, however, to the presence of backwardly directed barbs[1] on the overturned edges of the proximal barbules, which prevent the hamuli from slipping. These can only be effective against pressure from the underside of the feather. Yet they occur not only on the flight feathers, but also on some body feathers, where the pressure is only from above. This is admittedly remarkable, and according to Steiner can only mean that feathers arose and acquired their definitive structure on the arms.

With regard to the supposed mode of origin of feathers from scales, such general suggestions as have been put forward, for example by Davies and Gadow [7], are not satisfactory and fail to account for the aftershaft, a fundamental part of which all feathers preserve a trace at least in development. A scale, Steiner points out, is a flattened lamella cornified on both sides and with a more or less developed, permanent vascular core. The feather cannot correspond to the whole scale, but only to its outer half, the under surface of the feather corresponding to the inner surface of the cornified outer layers of the scale which was in contact with the vascular core, while the shaft is evidently derived from a strengthening ridge or keel which the scales of many present-day reptiles also exhibit. In a precisely similar

[1] The term 'barb' is here used in its ordinary descriptive sense, not to be confused with its special zoological sense as the English equivalent for the ramus of the feather.

way the aftershaft is held to represent the cornified layers of the under surface of the scale. As the scale became enlarged (in phylogeny) the vascular core must have become atrophied and the thin cornified upper and under layers of the palaeoptile could easily have become separated by wear at their edges, producing the main feather and the aftershaft. But this was mechanically an ineffective arrangement and the aftershaft quickly became reduced. As this reduction proceeded the incipient rami of the main feather, formed from oblique strengthening ridges analogous to the longitudinal ridge which formed the shaft, came to occupy correspondingly more and more of the circumference of the rudiment from which the palaeoptile developed. The rounded section of the feather rudiments of present-day forms must be secondary; in *Dromaeus*, which has a specially large aftershaft, the rudiment is more oval in section—i.e. it is nearer the flattened form of the scale.

Such in brief is Steiner's theory of the origin of feathers. It is frankly hypothetical, but in the absence of any actual ancestral stages any theory must necessarily be so, and it conforms to that type of 'judicious speculation' referred to at the outset as an essential part of phylogenetic inquiries, in that it accounts for the structure of modern feathers in a logical manner, and relates the morphological characteristics of feathers and scales in a reasonable and consistent way. That it is not, however, in the nature of the case conclusive almost goes without saying. An acceptance, for example, of the derivation of feathers from scales would not entirely exclude the possibility previously mentioned that this metamorphosis was initiated in adaptation to other needs than those of flight. It cannot be dogmatically asserted that the apparent transference of certain adaptive features from the flight feathers to the contour feathers and down absolutely proves that the former represent the ultimate ancestral type or wholly rules out the possibility that the features mentioned may have been superimposed on a still earlier type of feather structure. The uselessness for purposes of support of any feather-like structure lacking an interlocking mechanism, and the difficulty of seeing how such a mechanism could have been developed directly *ad hoc* in an effective form still constitute for the writer a real obstacle to the acceptance of any theory postulating the origin of feathers in direct adaptation

to affording support in the air (cf. p. 330). Nevertheless, it may be freely admitted that Steiner's arguments for regarding the structure of the quill feathers as genuinely primitive have very considerable weight. The writer does not feel that it is possible at present to arrive at a decision on the subject with any degree of certainty: the possibilities have been considered, and the reader must weigh them for himself.

The rejection of the theory of a terrestrial and cursorial Pro-avis leads naturally to the problem of the status of the Ratites, whose origin from primitively flightless terrestrial birds has been postulated in recent years by P. R. Lowe [9]. Those who are convinced by Steiner's arguments that the structure of feathers can only have been acquired in direct relation to the faculty of flight will need no further evidence against this hypothesis, but there are other objections which are less debatable. It is impossible here for reasons of space to examine the question at length, but it is desirable to allude to certain significant points which have not been made by other critics. As the writer has emphasized elsewhere [17], one of the weightiest of the many objections to Lowe's theory lies in the structure of *Archaeopteryx* and *Archaeornis*. All zoologists are agreed that these ancient birds were arboreal, and their well-developed wing quills make it quite certain that they could fly after a fashion, if not very effectively. Consequently Lowe's hypothesis entails the branching off of the Ratites from the avian stock long prior to the appearance of *Archaeopteryx*. But this makes it necessary to regard the whole array of characters wherein the Ratites agree with modern birds and differ from the Saururae, including the typically wing-like skeleton of the fore limb, as wholly convergent—and this notwithstanding that they have never flown! Exactly the same argument applies with even more force to the penguins, which Lowe [10] has also regarded as primitively flightless. He has directed attention to the bird-like characters of the hand of the dinosaur *Ornitholestes* as evidence that a bird-like hand can be developed independently of flight, but the writer has pointed out in the communication mentioned above that the resemblance is utterly superficial and that the peculiar bowing and terminal fusion of metacarpals 2 and 3 which characterize both the Carinate and the Ratite hand are in no wise reproduced in the dinosaur.

As to *Archaeopteryx* and *Archaeornis*, Lowe has sought to minimize the importance of these inconvenient animals by maintaining that they are so aberrant and reptilian that they cannot be on the main avian line at all. Considering that in spite of their essential similarity they are admittedly generically distinct, it would seem profoundly improbable on general grounds that these two forms, the only fossil birds known from the whole of the Jurassic, should both belong to a type not representative of the avifauna of the period, but there is a further piece of evidence which ought to be conclusive. This is the clear demonstration by Steiner from the relations and proportions of the feather imprints that *Archaeopteryx* and *Archaeornis* were diastataxic. The importance of this discovery does not seem to have been sufficiently recognized. It is completely incredible that so peculiar a condition as diastataxy can have arisen in an identical form twice over, and it is not too much to say that it is now absolutely certain that the Saururae are close to the main line of evolution of modern birds. Their structure can therefore by no means be disregarded in phylogenetic discussions concerned with the latter, and the case against the derivation of the Ratites from purely cursorial and non-flying ancestors is complete.

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LEIDEN: University Laboratory of Anatomy.
LIVERPOOL UNIVERSITY.
LONDON: John Innes Horticultural Institution.
LONDON: The Linnean Society.
LONDON: Royal College of Surgeons.
LONDON: St. Paul's School, West Kensington.
LONDON: South London Botanical Institute.
LONDON: University College.
LUCKNOW UNIVERSITY.
MELBOURNE UNIVERSITY.
MUSSELBURGH: Loretto School.
NAPLES: Stazione Zoologica.
OXFORD: Bureau of Animal Population, University Museum.
PARIS: Laboratoire d'Anatomie et d'Histologie comparées.
PARIS: Laboratoire de Paléontologie du Muséum.
PIETERMARITZBURG: Natal University College.
SHREWSBURY SCHOOL: The Darwin Science Society.
STOCKHOLM: Kungl. Vetenskapsakademiens Bibliotek.
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